Distribution of unionid mussels and sea lamprey larvae in relationship to habitat in streams of Lower Michigan and the Paw Paw River

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Abstract

Unionid mussels are critical to aquatic ecosystem function and are imperiled. They are indicators of biological integrity due to sensitivity to stressors and interconnectedness with the aquatic community. Like unionids, invasive sea lamprey larvae (Petromyzon marinus) burrow into stream sediments. Sea lampreys have seriously impacted the ecology of the Great Lakes. Sea lamprey control consists of lampricides targeting the larval stage (ammocoetes) in tributaries. Lampricides have sublethal effects on mussels. This study investigated mussel and ammocoete distribution and habitat use to aid in refining lampricide application. Habitat and mussel surveys were conducted in the Paw Paw River, in Southwest Michigan, and ammoceote data were obtained from databases of sea lamprey surveys conducted by the US Fish and Wildlife Service. Mussels were absent in most tributaries and had a mean density of 0.59/m² in the mainstem. Ammocoetes had a mean density of 0.43/m² and densities were highest in tributaries. A statewide regression analysis revealed that mussels have species specific distribution determinants and a canonical correspondence analysis demonstrated this species specific pattern in the Paw Paw River. Generalized linear models revealed median particle size, gradient, and bank stability to be effective predictors of unionid distribution in the Paw Paw River. Distance to sea lamprey spawning habitat and bank stability were effective predictors of ammocoete distribution. Minimal overlap of mussel and ammocoete distributions suggests that refinement of lampricide treatment in the Paw Paw River is possible. Redefining the extent of the mainstem reach and dividing it into several shorter reaches so that only areas with high ammocoete densities and low unionid densities would be treated with lampricide could result in reducing treatment costs and minimizing threats to unionid conservation while still having continued success in controlling sea lamprey.

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Overview

Unionid mussels are one of the most imperiled taxa in North America (Williams et al. 1993). In Michigan over 40% of species are state listed as endangered, threatened, or of special concern (Badra and Goforth 2003). Habitat destruction has been noted as a major driver in unionid population declines (Williams et al. 1993). Unionids are sensitive to stressors, both natural and anthropogenic. Because they require a fish host to disperse the larvae, mussels are highly interconnected with the aquatic community. Therefore, they are indicators of biological integrity and the status of unionid populations is indicative of the health of the system.

An additional threat to unionid mussels in the Great Lakes region is the chemical treatment of tributaries for invasive sea lamprey (*Petromyzon marinus*). Sea lamprey have serious impacts on the ecology of the Great Lakes region (Christie and Goddard 2003). The sea lamprey larvae (ammocoetes) spend approximately four years burrowed into stream sediments. Treatment of tributaries harboring ammocoetes with lampricides has been the preferred method of sea lamprey control. These control efforts have resulted in a 90% reduction in sea lamprey populations in most areas (Dawson 2007). These chemical treatments are intended to be selectively toxic to sea lamprey, though lethal and sub-lethal effects have been reported on other species (Gilderhus 1979, Gilderhus and Johnson 1980, US Fish and Wildlife Service Sea Lamprey Management Program 1996, Bills et al. 1992, Waller et al. 1997, Waller et al. 1998, Bogard et al. 2004, Hoggarth and Yankie, 2008). Unionid mussels may be particularly vulnerable to the nontarget effects of lampricides (Boogard et al. 2004). Previous studies have observed significant sub-lethal effects of lampricides on freshwater mussels. To date, no modifications to lampricide treatments have been made to minimize these negative effects to unionid mussels.

As unionid conservation plans are devised, an understanding of their distributions and habitat requirements are fundamental. Additionally, a comparison of habitat requirements and distribution of unionid mussels and ammocoetes is needed to determine the potential to refine lampricide treatments to protect mussel species while still achieving the benefits of sea lamprey control.

Objectives and hypothesis

The goal of this study was to investigate habitat requirements of unionid mussels and ammocoetes, compare distributions, and assess the potential to refine control methods to minimize negative effects to mussels. The objectives were to a) relate mussel species presence to landscape derived large scale habitat variables in Michigan's Lower Peninsula (Chapter 1), b) relate mussel species presence to local and landscape derived habitat variables in the Paw Paw River (Chapter 1 and 2), c) relate ammocoete presence to local and landscape derived habitat variables in the Paw Paw River (Chapter 2), and d) compare these relationships and make recommendations for refinement to lampricide treatments in the Paw Paw River (Chapter 2). It was hypothesized that unionid mussel and ammocoete distributions were influenced by different combinations of habitat variables and therefore, refinements to lampricide treatments were possible.

Chapter 1: Distribution of unionid mussels and habitat in Lower Michigan streams and in the Paw Paw River

Introduction

The North American unionid mussels are the most diverse among unionids in the world, with approximately 300 recognized species, 45 of which can be found in Michigan. However, unionid mussels are also one of the most imperiled groups in North America (Williams et al. 1993). Of the nearly 300 species, 37 are extinct, and about a third are considered imperiled or critically imperiled (Master et al. 2000). In Michigan, 19 of the 45 species - over 40% - are state listed as endangered, threatened, or of special concern (Badra and Goforth 2003). Decline of mussel populations is attributed directly to pollution and increases in siltation, controls of natural flow regimes (e.g., impoundments), loss of fish hosts, and competition and fouling by exotic species (Bogan 1993). The threat having the most impact on mussel populations, however, is habitat disturbance (Williams et al. 1993).

Unionids have many traits that render them vulnerable to habitat destruction. The life history of unionid mussels is complex. In the larval phase, they require a fish host. Larvae attach to the fish gills and are dependent upon the fish movement for dispersal. Once the larvae detach from the fish, and enter the juvenile stage, survival is poor. If they do survive beyond the juvenile stage, they are long-lived and slow to grow and consequently are susceptible to multiple stressors over time. Additionally, unionid mussels are sessile organisms that burrow into stream and lake sediments and have very limited mobility. These traits make unionids vulnerable to habitat loss and disturbance, but also make them indicators of biological integrity

(Metcalfe-Smith et al. 1997). Due to their sensitivity to stressors and interconnectedness with the aquatic community, a decline in mussel populations is an indication that the health of the system is at risk (Strayer 1999).

Unionid mussels provide considerable ecological benefits and are of conservation interest. Mussels have a functional role as filter feeders, filtering contaminants, nutrients, and sediments and improving water quality. They are a food source to many aquatic and terrestrial organisms. They are also sensitive to toxins and therefore, serve as an early warning of water quality concerns.

As unionid conservation plans are devised, an understanding of their distributions and habitat requirements is vital, particularly since degradation of habitat is the major driver in population declines. It is widely known that different species require different habitats (van der Schalie 1938, Strayer 1983, Huehner 1987, Cummings and Mayer 1992, Strayer 1993, McRae et al. 2004, Metcalf-Smith et al. 2005, Strayer 2008). Some, like *Pyganodon gradis,* prefer lotic environments or backwaters in streams with little or no current and mud or silt substrate (Cummings and Mayer 1992). Others, such as the endangered *Epioblasma torulosa rangiana,* prefer coarser sand and gravel substrates in riffle areas with swift currents (Metcalfe-Smith et al. 2005). Still others, for instance *Strophitus undulatus*, have broad distributions and are found in small to very large rivers, in a range of substrate and flow conditions (Metcalfe-Smith et al. 2005). However, both historical and recent characterizations of unionid habitat are contradicting and insufficient (Strayer 2008). Several studies indicated that local habitat measures like substrate particle size, instream cover (i.e. vegetation, woody debris) and current velocity could sufficiently characterize mussel habitat (van der Schalie 1938, Huehner 1987, Strayer and Ralley 1993, Hart 1995, Vaughn 1997). Yet, other studies showed that these local habitat metrics were not useful in predicting unionid mussel presence and abundance (Strayer 1981, Holland-Bartels 1990, Vaughn and Pyron 1995, Strayer 2008). Strayer and Ralley (1993) suggested that larger-scale habitat variables may be more effective predictors of mussel distributions in rivers. Large-scale variables such as surficial geology, stream size, and land cover were found to influence mussel presence and abundance (Strayer 1983, Strayer 1993, McRae et al. 2004). McRae et al. (2004) suggested that a combination of these local and large-scale habitat metrics best described mussel distributions.

In this study, the effectiveness of local and large-scale habitat variables in predicting the presence and abundance of mussel species was examined. It was hypothesized that mussel species' distributions were influenced by a combination of local and large-scale habitat variables. To test this hypothesis, two analyses were conducted. First, distributions of unionid species were investigated at a regional scale among streams in Michigan's Lower Peninsula using large-scale, landscape derived, habitat variables. Next, distributions were analyzed in the Paw Paw River using habitat variables measured at a local scale and large-scale variables derived from landscape characteristics. The objectives of this study were to: a) examine the influence of habitat variables on distributions of unionid species at a regional scale b) assess the status and abundance of mussel species in a selected stream, the Paw Paw River, and c) examine the influence of local and large-scale habitat variables on unionid species in the Paw Paw River.

Materials and Methods

Study Site

Data for this analysis are from streams located in the Lower Peninsula of the State of Michigan. Michigan has 58,500 km of rivers and streams. In the Lower Peninsula, these streams comprise over twenty major river systems that empty into Lake Michigan, Lake Huron, and Lake Erie (Seelbach and Wiley 1997). Mussel data were available for fourteen major watersheds in the Lower Peninsula - the Muskegon River, Grand River, Rifle River, Shiawassee River, Titabawassee River, Cass River, Kalamazoo River, Huron River, River Raisin, Clinton River, Black River, Belle River, Galien River, and Saint Joseph River (Fig. 1). The selected watersheds make up the southern and middle portion of Michigan's Lower Peninsula. The majority of the streams in this part of the state of Michigan have low gradient ranging from less than 0.8m/km to 1.9m/km. The selected watersheds are mostly cool to warm water systems, with the exception of the Muskegon River which is a cold to cool water system (Seelbach et al. 1997).

The Paw Paw River, selected as a case study, is the northern-most tributary of the St. Joseph River located in Southwest Michigan (Fig. 2). The St. Joseph watershed is one of the largest in the Lower Peninsula draining 12,134 km^2 into Lake Michigan. The Paw Paw watershed covers approximately 715 km^2. The mainstem and lower reaches of the Paw Paw River have cool mean water temperatures with modeled July weekly mean temperatures between 19°C and 22°C, and are runoff driven (Seelbach et al. 1997). The upper reaches and tributaries have cold mean water temperatures with lower modeled July weekly mean temperatures between 14°C and 19°C and are groundwater driven (Seelbach et al. 1997). Much of the watershed's channels are composed of sand. Headwaters have a baseflow of up to 0.5 m^3/s, while the mainstem baseflow ranges between 5.7 and 12.7 m^3/s (Michigan Department of Information Technology, Center for Geographic Information (http://www.mcgi.state.mi.us/mgdl)). Farmland, orchards, and vineyards make up the majority of the land cover in the watershed.

Unionid mussel and habitat data at the regional scale

Regional scale unionid mussel data were available from the Michigan Natural Features Inventory (MNFI) database. The database contains information only on species listed by the state of Michigan as endangered, threatened or of special concern. Data consist of presence and absence for 17 listed unionid species in 431 locations, along 14 major rivers surveyed in Michigan's Lower Peninsula between 1917 and 2006 (Fig. 1). For the analysis, only the nine most common listed species were selected as other species were mostly absent within the sampling sites. Selected species were: *Alasmidonta viridis* (slippershell mussel), *Alasmidonta marginata* (elktoe), *Epioblasma triquetra* (snuffbox), *Cyclonaias tuberculata* (purple wartyback), *Pleurobema sintoxia* (round pigtoe), *Villosa iris* (rainbow), *Venustaconcha ellipsiformis* (ellipse), *Villosa fabalis* (rayed bean), and *Lampsilis fasciola* (wavyrayed lampmussel).

Habitat data available at the state level were from the Michigan Department of Natural Resources Landscape-Based Ecological Classification System for River Valley Segment Classification (MI-VSEC) database (Seelbach et al. 1997). The database contained landscape habitat variables at the resolution of valley segments, defined as "structurally homogeneous" and "ecologically distinct" spatial units along a stream. These units can be quite large ranging from 3 to 60 km in length (Seelbach et al. 1997). The following MI-VSEC variables were used as predictors in the models: modeled temperature, valley origin, hydrology, and gradient. For the purposes of this study, I rescaled the original MI-VSEC variables before including them in the models (Table 1, Fig. 3). Temperatures were modeled based on catchment size, hydrology, and distribution of cold and warm water fishes (Seelbach et al. 1997). I consolidated the original nine levels for modeled temperature from Seelbach et al. (1997) into three – cold (14 - 19°C), cool (19 - 22°C), and warm (22 - 26°C). Valley character described channel confinement and valley origin. I consolidated the original eight levels from Seelbach et al. (1997) into the two valley origin levels – alluvial and glacial. Valley origin described how the river was formed, where alluvial channels were carved out by the current river and glacial valley channels were carved out by a glacial meltwater river thousands of years ago (Seelbach et al. 1997). Hydrology described whether the valley segment was groundwater or runoff-driven and the intensity of base and peak flows. I consolidated the original seven levels from Seelbach et al. (1997) into two – groundwater-driven or runoff-driven. Lastly, gradient, which described the slope of the valley segment, originally had three levels - moderate (> 1.9m/km), low (0.8 – 1.9 m/km), or very low (< 0.8 m/km). However, only the low and very low levels were used in this analysis as less than 2% of the data points were located in moderate gradient. Habitat variables and MNFI listed mussel data were linked using georeferenced locations and ArcMap v. 9.3.1 (ESRI 2009).

Analysis of Lower Michigan unionid distribution in relationship with habitat was conducted using a regression model approach. Generalized linear models (GLM) (McCullagh and Nelder 1989) were implemented for the distribution of each of the nine species selected. Routines available in the S-PLUS computing environment were used to conduct the analysis (TIBCO Software Inc. 2007). Presence of each species was modeled as a function of temperature, valley origin, hydrology, and gradient and incorporating a binomial probability distribution to relate the response and predictors as follows:

$$g(\mu_{tvhd}) = \alpha + \lambda_t + \delta_v + \xi_h + \zeta_d \qquad (1)$$

where g() was the logit link function $\ln[\mu_{tvhd} /(1- \mu_{tvhd})]$, μ was the expected probability of unionid species presence in temperature conditions represented by t, valley origin type represented by v, hydrology conditions represented by h, and gradient represented by d. All predictor variables were introduced as factors.

Unionid mussel and habitat data from the Paw Paw River

During this study, 45 sites were surveyed in the Paw Paw River (Fig. 2) to determine mussel distribution and characterize stream habitat. Surveys were conducted between June and October 2009, in wadable areas of the river. Location of the sites, though influenced by accessibility, was chosen to achieve a representative sample of the watershed's surficial geology, and to obtain a spatial representation of the entire Paw Paw system. Site location was also based on the location of historical surveys to evaluate the distribution of sea lamprey larvae (ammocoetes) as the study also included a comparison in distribution and habitat requirements of unionids and ammocoetes (see Chapter 2). Sites on tributaries of the Paw Paw River were within a distance of 10 to 100 m from the road crossings used for access. Most sites on the mainstem were not accessible from a road crossing and were accessed using a canoe.

At each survey location, data on qualitative habitat assessment, substrate and unionid mussel densities were recorded. The qualitative habitat assessment was performed using the Ohio EPA's Qualitative Habitat Evaluation Index (QHEI) (Rankin 1989, Ohio EPA 2006). To calculate this index, substrate quality, instream cover, channel morphology, bank stability, riparian zone, and pool and riffle quality were visually scored in the field. Scoring of substrate quality was based on visual assessments of substrate types, the origin of the stream substrate, and the degree to which substrates were impacted or covered by fine materials. Scoring of instream cover was based on visual assessments of the type and amount of instream cover available. Scoring of channel morphology was based on visual assessments of channel sinuousity and stability. Scoring of bank stability was based on visual assessments of bank erosion. Scoring of riparian zone was based on visual assessments of riparian width and floodplain quality. Scoring of pool and riffle quality was based on a visual assessment of pool and riffle widths and current velocity. The last metric score was based on gradient (m/km) and drainage area (km^2) which were available from the MI-VSEC database (Seelbach et al. 1997). All metrics received individual scores that were totaled for a maximum of 100 points at each site.

Substrate composition in terms of particle size was measured by visual inspection based on percent coverage of boulder (diameter > 256mm), cobble (256-64mm), pebble (64-16mm), gravel (16-2mm), sand (2-0.0625mm), and silt (<0.0625mm). Percentage of each substrate size was then used to calculate median particle size.

Pebble counts were performed and used to validate the accuracy of the visual estimation at the first 25 sites (Wolman 1954). For validation, samples were collected by walking from bank to bank in an upstream direction. The first particle touched at each step was measured with a gravelometer. When 100 particles were measured, the counter completed the crossing to the other side of the channel (Wolman 1954, Kondolf 1997). Estimates of substrate composition based on visual inspection compared to pebble counts in the 25 validation sites were similar (Chi-square test, p=0.282) and in the rest of the sites, substrate was assessed exclusively by visual inspection.

Surficial geology (Michigan Quaternary Geology) data for the Paw Paw River watershed were available from Michigan Department of Information Technology, Center for Geographic Information (http://www.mcgi.state.mi.us/mgdl). Surficial geology, in addition to the MI-VSEC variables used in the regional analysis (hydrology, gradient, valley origin, and modeled temperature) were linked to the 45 sites surveyed using ArcMap v. 9.3.1 (ESRI 2009).

Unionid mussels were identified to species and enumerated within an area of 128 m^2 at each survey site. If an area this size was not wadable, the largest wadable area was surveyed. The entire selected area was searched for live mussels and empty shells tactilely and visually with the use of glass bottom buckets. This is a well established method of increasing visual detection of mussels and a widely used technique for mussel surveys (Badra and Goforth 2003, Strayer and Smith 2003, McRae et al. 2004). Live mussels were measured lengthwise from posterior end to anterior end.

Historical unionid mussel data for 7 sites in the Paw Paw watershed from the University of Michigan Museum of Zoology database and collected between 1918 and 1934 (Fig. 4) were used to compare to current unionid populations. Three of these sites were located on lakes within the Paw Paw watershed, and the other 4 sites were located on the mainstem of the river. Only one historical site overlapped with the survey sites of the current study.

A canonical correspondence analysis (CCA) was used to relate species' distribution based on densities of selected species to environmental variables. A CCA is a multivariate direct gradient analysis (ter Braak 1986). All 45 sites were included in the CCA. The four most common species, *Elliptio dilatata* (spike), *Fusconaia flava* (wabash pigtoe), *Venustaconcha ellipsiformis* (ellipse), and *Amblema plicata* (threeridge) were selected for the analysis as remaining species were found at less than 4% of the total sites and at low densities less than $0.03/m^2$. Environmental variables in the CCA analysis were QHEI instream cover score, QHEI channel morphology score, QHEI bank stability score, QHEI riparian zone score, gradient (m/km), drainage area, median particle size, and surficial geology. QHEI substrate quality score was not included in the analysis because it was significantly ($p<0.05$) correlated with median particle size ($r = 0.84$). QHEI gradient/drainage area score was not included in the CCA as it was significantly correlated with gradient (m/km) ($r = 0.67$). Also total QHEI score was not included in the CCA as it was significantly correlated with QHEI substrate quality score ($r = 0.60$), QHEI instream cover score ($r = 0.68$), and QHEI channel morphology score ($r = 0.67$). QHEI pool and riffle quality score was also not included as there was almost no variability in scores across all sites. The MI-VSEC variables – hydrology, gradient, valley origin, and modeled temperature – were not included in the CCA because the scale of valley segments was too coarse for the Paw Paw River and there was very little or no variability within sites where mussel surveys were conducted. The CCA was run using CANOCO 4.0 software (ter Braak and Smilauer 1998) which ordered the habitat variables by their ability to describe the variance in species' densities. A forward selection procedure was used to identify those habitat variables accounting for the greatest amount of variation. Those variables were tested for significance ($p < 0.05$) in 1000 Monte Carlo simulations before being included in the model (ter Braak and Smilauer 1998).

To aid interpretation of unionid distributions, known host fish species distributions were mapped for the most common unionid species, *Elliptio dilatata, Fusconaia flava, Amblema plicata,* and *Venustaconcha ellipsiformis* in the Paw Paw River. Known host fish species in the Paw Paw River included yellow perch (*Perca flavescens*), white crappie (*Pomoxis annularis*), black crappie (*P. nigromaculatus*), bluegill (*Lepomis macrochirus*), pumpkinseed (*L. gibbosus*), rock bass (*Ambloplites rupestris*), black-sided darter (*Percina maculata*), rainbow darter (*Etheostoma caeruleum*), johnny darter (*E. nigrum*), mottled sculpin (*Cottus bairdi*), and brook stickleback (*Culaea inconstans*). Data on host fish distributions were from the Atlas of Michigan Fishes, University of Michigan Museum of Zoology.

Results

Of the 9 listed unionid species selected for regional analysis, *Alasmidonta viridis,* present in 27.15% of the total sites, was the most often found. Occurrence of this species was closely followed by *A. marginata* and *Villosa iris,* while *V. fabalis,* present at 5.80% of the total sites, had the lowest probability of being found (Table 2).

The distribution of 7 of the 9 selected listed mussel species - *Alasmidonta viridis, A. marginata, Epioblasma triquetra, Cyclonaias tuberculata, Villosa iris, V. fabalis,* and *Lampsilis fasciola* – were significantly dependent upon one or more of the following landscape habitat variables: temperature, valley origin, and gradient. These 7 species had distinct distributions with respect to the habitat variables (Table 2 and 3). Gradient, valley origin, and temperature were significant predictors for presence of *Alasmidonta viridis* with a higher probability of occurrence in streams of alluvial origin and with low gradient and cold water (Table 2, Fig. 5). Valley origin and temperature were significantly associated with *Alasmidonta marginata* presence, where probability of occurrence was higher in streams of glacial origin, with cool to warm water (Fig. 6). *Epioblasma triquetra* occurrence was higher in streams with very low gradient (Fig. 7). *Cyclonaias tuberculata* presence was significantly higher in cool to warm water streams (Fig. 8). There was a significantly higher probability of *Villosa iris* occurrence in streams of alluvial origin (Fig. 9). *Villosa fabalis* presence was significantly higher in warm water streams with very low gradient (Fig. 10). Probability of *Lampsilis fasciola* presence was higher in cool to warm water streams with low gradient (Fig. 11).

Of the four MI-VSEC landscape habitat variables included in the analysis, modeled temperature was the most often significant predictor of listed mussel presence at the regional level. It was a significant predictor in the *Alasmidonta viridis, A. marginata, Cyclonaias tuberculata, Villosa fabalis,* and *Lampsilis fasciola* models (Table 3). These species, with the exception of *Alasmidonta viridis,* had a higher probability of occurrence in cool to warm water streams (modeled temperatures > 19°C). *Alasmidonta viridis* was more likely to occur in cold water streams (modeled temperatures between 14°C and 19°C). Also, temperature accounted for most of the explained deviance in these models, with the exception of *Alasmidonta marginata* where valley origin was more important. Hydrology was not a significant predictor in any of the species distributions, possibly because most streams surveyed were runoff driven. None of the MI-VSEC variables were significant predictors of *Pleurobema sintoxia* or *Venustaconcha ellipsiformis* presence. Though some variables were significant predictors of listed mussel species presence, only 0.78% to 12.23% of the deviance was explained by these models (Table 3).

In the Paw Paw River, live mussels were found at 17 of the 45 sites and at an additional 10 sites, only shells were found. Most sites where live individuals were counted were located on the mainstem of the Paw Paw River (Fig. 12). A total of 842 live unionid mussels were counted representing 9 species. Additionally, 8 species were found as shells. The mean density of all species combined was 0.59 individuals/m^2 at sites where live individuals were present reaching a maximum of 5.09/m^2. The number of live species per site ranged from 0 to 7 with a mean of 3 (Fig. 13).

Elliptio dilatata was the most abundant and most widely distributed species, representing approximately 79% of the total abundance, followed by *Fusconaia flava, Venustaconcha ellipsiformis* and *Amblema plicata.* These four species together accounted for 98.4% of the total abundance. The remaining five species were found in very low densities and at only one or two sites (Table 4). The state endangered *Toxolasma parvus* and the state threatened *Alasmidonta viridis* were only found as shells. Additionally, four species of special concern were found – *Venustaconcha ellipsiformis* (live), *Pleurobema sintoxia* (live), *Villosa iris* (live), and *Alasmidonta marginata* (shell) (Table 4).

Historical records indicate the presence of 17 species in surveys conducted between 1918 and 1934 in the Paw Paw River. The current study found 9 of these species live and 7 as shells. *Lasmigona complanata* was found historically but not during the current study. However, *Toxolasma parvus*, a state endangered species, was not in the historical records but was found as a shell during the present study (Table 5).

Results from the CCA indicated that four habitat variables significantly ($p<0.05$) accounted for the variance in *Elliptio dilatata, Fusconaia flava, Venustaconcha ellipsiformis,* and *Amblema plicata* densities. Bank stability, gradient, drainage area, and median particle size together explained 40% of the variance in the four most common species' densities. As indicated by the longer rays in the CCA biplot illustrating where these species fall on the environmental gradients (Fig. 14), drainage area and bank stability were major variables producing gradients among the mussel species. *Elliptio dilatata* densities were somewhat aligned with larger median particle size and lower bank stability. *Elliptio dilatata* is the most centrally located of the four species on the biplot and therefore, is the most tolerant species occurring in a larger range of these environmental variables. *Fusconaia flava* was positively aligned with bank stability and gradient, and negatively with drainage area and median particle size. *Venustaconcha ellipsiformis* was positively aligned with drainage area and bank stability and negatively aligned with median particle size and gradient. As indicated by its position on the biplot, *Amblema plicata* was closely aligned with high bank stability and drainage area, and with smaller median particle size and low gradient.

In the Paw Paw River, there are known records for the presence of host fish species for the four most common mussel species found in this study: *Elliptio dilatata, Fusconaia flava*, *Amblema plicata* and *Venustaconcha ellipsiformis* (Watters 1994, Mulcrone 2006). The host fish of *Elliptio dilatata* were reported throughout the mainstem and in the upper reaches of the Paw Paw River, overlapping with the distribution of *Elliptio dilatata* (Fig. 15). The host fish of *Fusconaia flava* were also reported throughout the mainstem and the North Branch, with considerable overlap with distribution of *Fusconaia flava* (Fig. 16). The distribution of *Amblema plicata* was more restricted than the distribution of its host reported throughout the mainstem, upper reaches and some of the tributaries (Fig. 17). The host fish of *Venustaconcha ellipsiformis* were reported throughout the mainstem, the North Branch, and some tributaries, considerably overlapping with the distribution of *Venustaconcha ellipsiformis* (Fig. 18).

Discussion

In the Lower Michigan streams represented in this study, unionid species tended to differ in their large-scale habitat preferences. Of the nine selected species, seven correlated significantly with at least one of the habitat variables - gradient, temperature, and valley origin. Temperature was the most important predictor of mussel presence followed by gradient. Strayer (1993) showed that macrohabitat variables, including gradient and hydrology, predicted species presence in streams of the northern Atlantic Slope. He found that gradient predicted the presence of two species of *Alasmidonta* and these species were more likely to occur in sites with relatively high gradient. Consistent with these results, *Alasmidonta viridis* was more often found in sites with relatively higher stream gradient (low as opposed to very low) in Lower Michigan; though gradient in Lower Michigan streams is far lower than gradient in streams of the northern Atlantic Slope. Hydrology was not a significant predictor of mussel species distributions in this study as nearly 90% of the sampling sites were located in runoff driven stream VSECs.

Valley origin was a significant model predictor for the presence of three listed species in Lower Michigan streams. Previous studies suggested that geology plays an important role in mussel distributions (Strayer 1983, McRae et al. 2004). However, Strayer (1983) indicated that it is the local habitat variables which are linked to the geological patterns that actually influence distribution. Geology affects substrate sizes, gradient, and channel morphology, and subsequently discharge. The glacial or alluvial valley origin is determined by the underlying geological pattern and, in turn, has significant influence on local habitat (Seelbach et al. 1997).

Hydrology, gradient, temperature, and valley origin, although significant in predicting the distribution of listed unionid species, were not able to account for much of the variation in their distributions. This could be because when analyzing rare species distributions, there is little data to compare. A similar analysis using common species presence and distribution in Michigan's Lower Peninsula may have produced stronger results; however, data on common species were not available at the state level.

Local-scale habitat variables are needed in addition to large-scale variables in predictive models of unionid species' distributions in Lower Michigan streams as elsewhere. McRae et al. (2004) found that a combination of reach and catchment scale variables significantly predicated unionid distributions in the River Raisin in Southeast Michigan. In the Paw Paw River, a CCA demonstrated that the four most common species' distributions were significantly influenced by both large-scale habitat variables (drainage area and gradient) and local-scale habitat variables (median particle size and bank stability). Bank stability appeared to be the most important local-scale variable. Bank stability represents the hydrologic stability and some mussel species prefer a hydrologically stable environment (Strayer 1999, Mcrae et al. 2004, Strayer 2008). However, others, like *Amblema plicata* and *Fusconaia flava,* are thick-shelled species and have more mass; thus, are likely more tolerant of relatively unstable hydrology and scouring.

Consistent with previous studies, drainage area was found to be strongly related to distribution of the four most common unionid species in the Paw Paw River. Strayer (1983) demonstrated similar species specific preferences for drainage area in Southeastern Michigan streams. The author found that *Elliptio dilatata* tolerated a wide range of drainage areas (50 –

3000 km^2), while *Amblema plicata* preferred slightly larger drainage areas (120 – 3000 km^2). It is likely that it is not the extent of the drainage area but rather the many physical habitat variables linked to drainage area (i.e. substrate size, current velocity, temperature) that are the factors determining distributions (Vannote et al. 1980, Strayer 1983).

Particle size was also a significant factor describing unionid distributions in the Paw Paw River in the current study, and was shown to control unionid species distributions in previous studies (Huehner 1987, Hart 1995, Badra and Goforth 2003, McRae et al. 2004). The current study found *Amblema plicata* and *Fusconaia flava* to be more tolerant of relatively smaller median particle sizes - sand (diameter = 0.0625 - 2mm) and gravel (2 – 16mm) mixes. Hart (1995) and McRae et al. (2004) also found these two species to be associated with sand and gravel substrates. In the Paw Paw River *Venustaconcha ellipsiformis* and *Elliptio dilatata* were generally found in sites with larger median particle sizes - sand, gravel, and pebble (16 – 64mm) mixes. Huehner (1987) had similar results with *Elliptio dilatata*. Many sites in the Paw Paw River were composed of mostly (>80%) unstable, flowing sand. These sites typically did not support any mussel species. Badra and Goforth (2003) had similar observations.

Presence and distribution of host fish species, which play an important role in determining mussel distributions (Strayer 2008), did not seem to be restricting distributions of the most common unionid species in the Paw Paw River in this study. The distribution range of *Amblema plicata,* in particular, was much more limited than that of its hosts. This is evidence that this species' distribution is not restricted by its host, but by other variables. Strayer (1983) found very similar results with *Amblema plicata* in streams in Southeastern Michigan.

Some species in the mussel community are thriving in the Paw Paw River while they are imperiled elsewhere. *Elliptio dilatata,* though very abundant and widely distributed in the Paw Paw River, is imperiled in Illinois systems (NatureServ.org). Juvenile *Elliptio dilatata* were found in the middle of the mainstem at a site with low gradient, a relatively high percentage of gravel and pebble substrate, some riffle habitat, and stable banks. This, in addition to the high densities found, is strong evidence that the population is thriving and reproducing. A species of special concern in Michigan, *Venustaconcha ellipsiformis,* was the third most abundant and second most widely distributed species in the Paw Paw River. This reflects the healthiness of the Paw Paw River and makes it worthy of conservation efforts.

The presence of shells in the survey added information on the depressed status of numerous species in the Paw Paw River. Though most species found historically in the Paw Paw River were found in the current survey, almost half were found only as shells. The presence of a shell could mean that there are live individuals in the system, but the survey was unable to locate them because of their very low numbers. It could also imply that there is no longer a viable population. Further, the presence of a shell suggests that the species was present nearby the survey location within the last 20 years (Carroll and Romanek 2006), with timing depending on the conditions of the stream which determine how long it takes for the shell to degrade (i.e. pH, calcium, current speed) (Strayer and Malcom 2007).

The results from this study can be affected by the survey location. Because survey site selection was highly dependent upon access and wadability in the Paw Paw River, unionid mussels living at depths greater than 1m were not surveyed. Unionid mussels are known to live at these greater depths in riverine environments (Hart 1995); however, the distribution and habitat preferences for unionids deeper than 1m in the Paw Paw River were not assessed.

Results from unionids surveys in the Paw Paw River may be limited by the search methods utilized. Unionid survey methods in the Paw Paw River consisted of a visual a tactile search, without excavating the substrate. Studies have shown that excavation of the substrate will locate increased numbers of juveniles and smaller species (Smith et al. 1999, Smith et al. 2001). However, concern over habitat destruction from excavation kept the search methods to a visual and tactile search without excavating the substrate.

Results of the regional and local scale analysis for the two species found in the Paw Paw River and among the Michigan Lower Peninsula streams in this study (*Venustaconcha ellipsiformis*, and *Pleurobema sintoxia)* were fairly consistent. The results of the regional analysis, though not significant, indicated that *Venustaconcha ellipsiformis* was most often found in runoff driven systems of alluvial origin, with cool to warm waters. Consistent with this, in the Paw Paw River, this species was only found in runoff driven sites of alluvial origin and mostly in cool waters. On the other hand, in the Paw Paw River, this species was significantly negatively aligned with gradient while presence in low (0.8 – 1.9m/km) and very low (<0.8m/km) gradient streams at the regional scale did not vary. However, the regional analysis was only concerned with gradients between 0.8 and 1.9m/km and the gradient in the Paw Paw River ranged from 0.04 - 4.4m/km. Therefore, the range of gradient explored in the regional analysis and the scale of the regional analysis were not sufficient to detect gradient preferences for *Venustaconcha ellipsiformis*. For *Pleurobema sintoxia,* results of the regional analysis demonstrated that the species was most often found in low gradient (0.8 – 1.9m/km), cool to warm waters of glacial origin sites. In the Paw Paw River, this species was only found at one site which was located on a cool water VSEC, but of alluvial origin. Although results from both analyses were not fully consistent, regional trends were not significant.

Habitat disturbance has impacted freshwater mussel populations more than any other threat (Williams et al. 1993). In order to conserve freshwater mussel populations, managers must protect the mussel habitat. Conservation management can happen at many spatial scales. The current study investigated distributions and habitat of unionid species at the regional scale, and the watershed scale. The results at both spatial scales indicated that habitat use is largely species specific. When this mussel habitat is conserved, biodiversity and stream health, in addition to the mussels themselves, are conserved.

Table 1. – Original (Seelbach and Wiley 1997) and rescaled MI-VSEC variable levels.

	Description of Original Levels	**Rescaled Levels**
Temperature	Cold, cool, or warm mean modeled temperatures with low to high diurnal variation (9 levels)	Cold, cool, warm
Valley character	Glacial or alluvial valley origin and degree of channel confinement (8 levels)	Glacial, alluvial
Hydrology	Groundwater or runoff-driven with very low to very high base and peakflows (7 levels)	Groundwater, runoff
Gradient	Medium (>1.9Mm/km), Low (0.8 - 1.9m/km) or Very Low (<0.8m/km) (3 levels)	Low, very low

*Valley character was re-labeled valley origin for the current analysis as the rescaled levels consisted of only valley origin information

Table 2. – Analysis of deviance for binomial generalized linear models for presence of listed mussel species in selected streams in Michigan's Lower Peninsula as a function of hydrology, gradient, valley origin and modeled temperature. * indicates that the variable is significant at the p<0.05 level.

			Percent deviance explained by variables				
Species	**Proportion of sites present**	**Null deviance**	**Total**	**Hydrology**	**Gradient**	**Valley origin**	**Temp**
Alasmidonta viridis	0.27	484.01	6.27%	0.40%	*0.87%	*1.03%	*3.97%
Alasmidonta marginata	0.27	482.00	4.06%	0.21%	0.14%	*2.31%	*1.40%
Epioblasma triquetra	0.09	244.81	7.59%	0.70%	*4.71%	0.36%	1.81%
Cyclonaias tuberculata	0.11	272.01	7.30%	0.56%	0.62%	0.76%	*5.36%
Pleurobema sintoxia	0.21	426.19	0.78%	0.00%	0.43%	0.23%	0.12%
Villosa iris	0.24	469.46	2.42%	0.00%	0.32%	*1.36%	0.74%
Venustaconcha ellipsiformis	0.11	272.01	1.99%	0.13%	0.00%	0.20%	1.66%
Villosa fabalis	0.06	188.93	12.23%	0.00%	*2.74%	0.69%	*8.81%
Lampsilis fasiola	0.14	339.37	10.26%	0.63%	*4.16%	0.75%	*4.72%

Table 3. – Coefficients for binomial generalized linear models for presence of listed mussel species in selected streams in Michigan's Lower Peninsula as a function of hydrology, gradient, valley origin and modeled temperature. Predictors are 2 and 3 level factor variables: hydrology (ground-water, runoff), gradient (low, very low), valley origin (alluvial, glacial), temperature (cold, cool, warm). Coefficients are on the logit scale. Coefficients for each factor represent the difference with the first level included within the intercept. * indicates that this difference is significant at the p<0.05 level.

Species	Intercept	Hydrology	Gradient	Valley origin	Temp
Alasmidonta viridis	0.851	-0.719	*-0.300	*-0.679	*cool: -0.393 warm: -1.134
Alasmidonta marginata	-1.964	-0.602	-0.238	*0.795	*cool: 1.306 warm: 1.512
Epioblasma triquetra	-14.651	6.044	*1.186	-0.264	cool: 5.677 warm: 5.623
Cyclonaias tuberculata	-15.074	5.877	-0.618	0.607	*cool: 6.694 warm: 7.396
Pleurobema sintoxia	-1.550	0.003	-0.319	0.269	cool: 0.311 warm: 0.322
Villosa iris	-0.041	-0.071	-0.362	*-0.700	cool: -0.763 warm: -0.591
Venustaconcha ellipsiformis	-3.885	0.640	0.003	-0.160	cool: 1.535 warm: 1.057
Villosa fabalis	-10.468	0.102	*0.421	-0.551	*cool: -0.197 warm: 7.892
Lampsilis fasciola	-14.791	6.215	*-1.266	-0.296	*cool: 7.711 warm: 7.560

Table 4. – Mussel species status in the State of Michigan, species abundance, percent of total sites live species were found and mean species densities in the Paw Paw River.

Species	**State Status**	**% total abundance**	**% sites present**	**Mean density (ind./m^2)**
Elliptio dilatata	Unranked	79.3%	35.6%	0.475
Fusconaia flava	Unranked	14.1%	20.0%	0.140
Venustaconcha ellipsiformis	Special Concern	4.1%	22.2%	0.047
Amblema plicata	Unranked	0.9%	4.5%	0.033
Strophitus undulatus	Unranked	0.5%	2.2%	0.031
Lampsilis siliquoidea	Unranked	0.4%	4.4%	0.017
Lasmigona costata	Unranked	0.2%	2.2%	0.013
Pleurobema sintoxia	Special Concern	0.2%	2.2%	0.037
Villosa iris	Special Concern	0.2%	2.2%	0.037
Lasmigona compressa	Unranked	Shell	Shell	Shell
Anodontoides ferussacianus	Unranked	Shell	Shell	Shell
Pyganodon grandis	Secure	Shell	Shell	Shell
Alasmidonta viridis	Threatened	Shell	Shell	Shell
Lampsilis ventricosa	Unranked	Shell	Shell	Shell
Actinonaias ligamentina	Unranked	Shell	Shell	Shell
Alasmidonta marginata	Special Concern	Shell	Shell	Shell
Toxolasma parvus	Endangered	Shell	Shell	Shell

Table 5. – Mussel species found historically in the Paw Paw River between 1918 and 1934 (7 sites) compared to those found during the current study (45 sites).

Historical records	**2009 survey**
Elliptio dilatata	live
Fusconaia flava	live
Venustaconcha ellipsiformis	live
Amblema plicata	live
Strophitus undulatus	live
Lampsilis siliquoidea	live
Lasmigona costata	live
Pleurobema sintoxia	live
Villosa iris	live
Lasmigona compressa	shell
Anodontoides ferussacianus	shell
Pyganodon grandis	shell
Alasmidonta viridis	shell
Lampsilis ventricosa	shell
Actinonaias ligamentina	shell
Alasmidonta marginata	shell
Lasmigona complanata	absent

***** *Toxolasma parvus* was not in historical records, but was found in the current study as a shell.

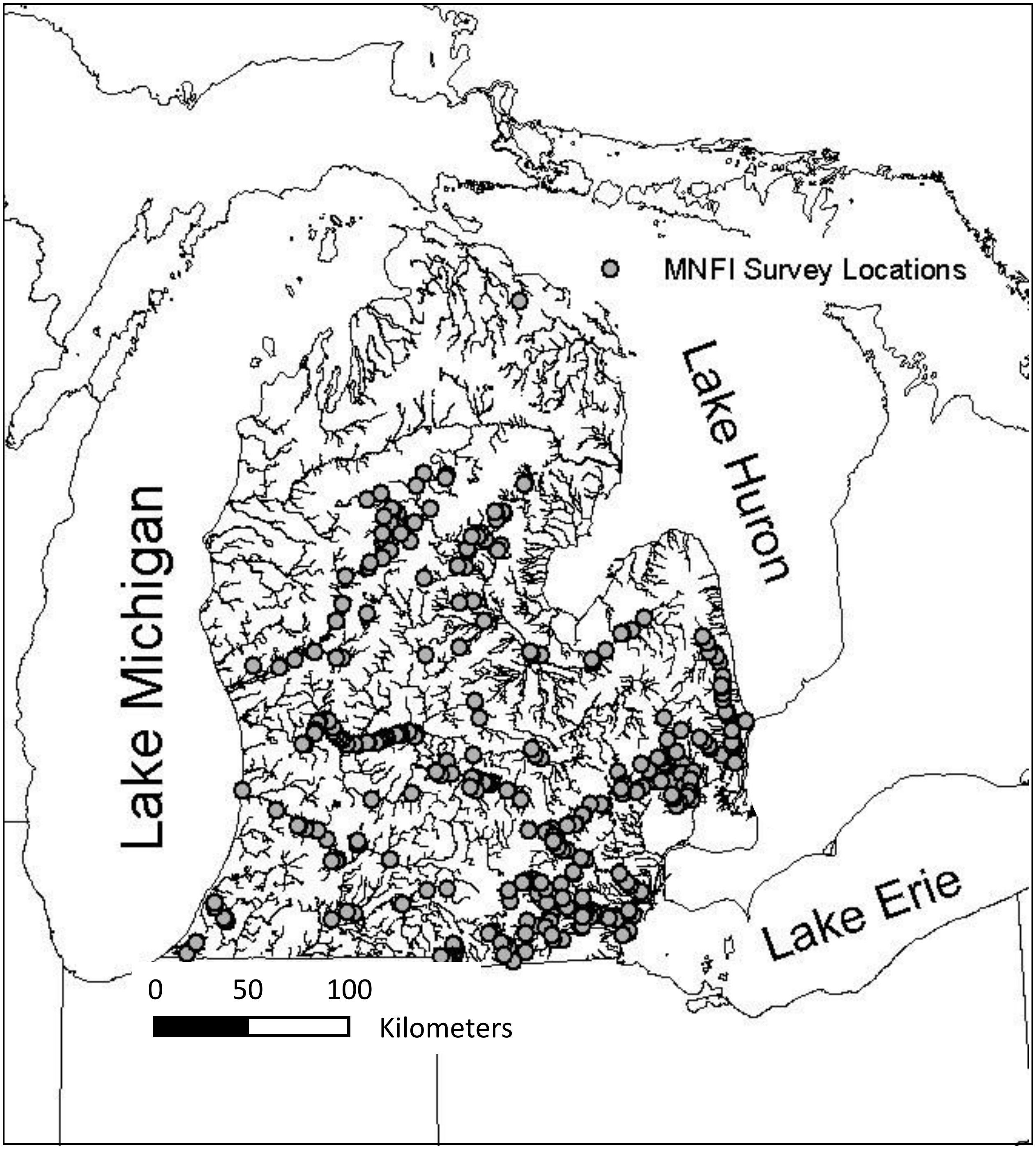


Figure 1. – Map of mussel survey sites in Michigan's Lower Peninsula from the Michigan Natural Features Inventory (MNFI) used in this study.

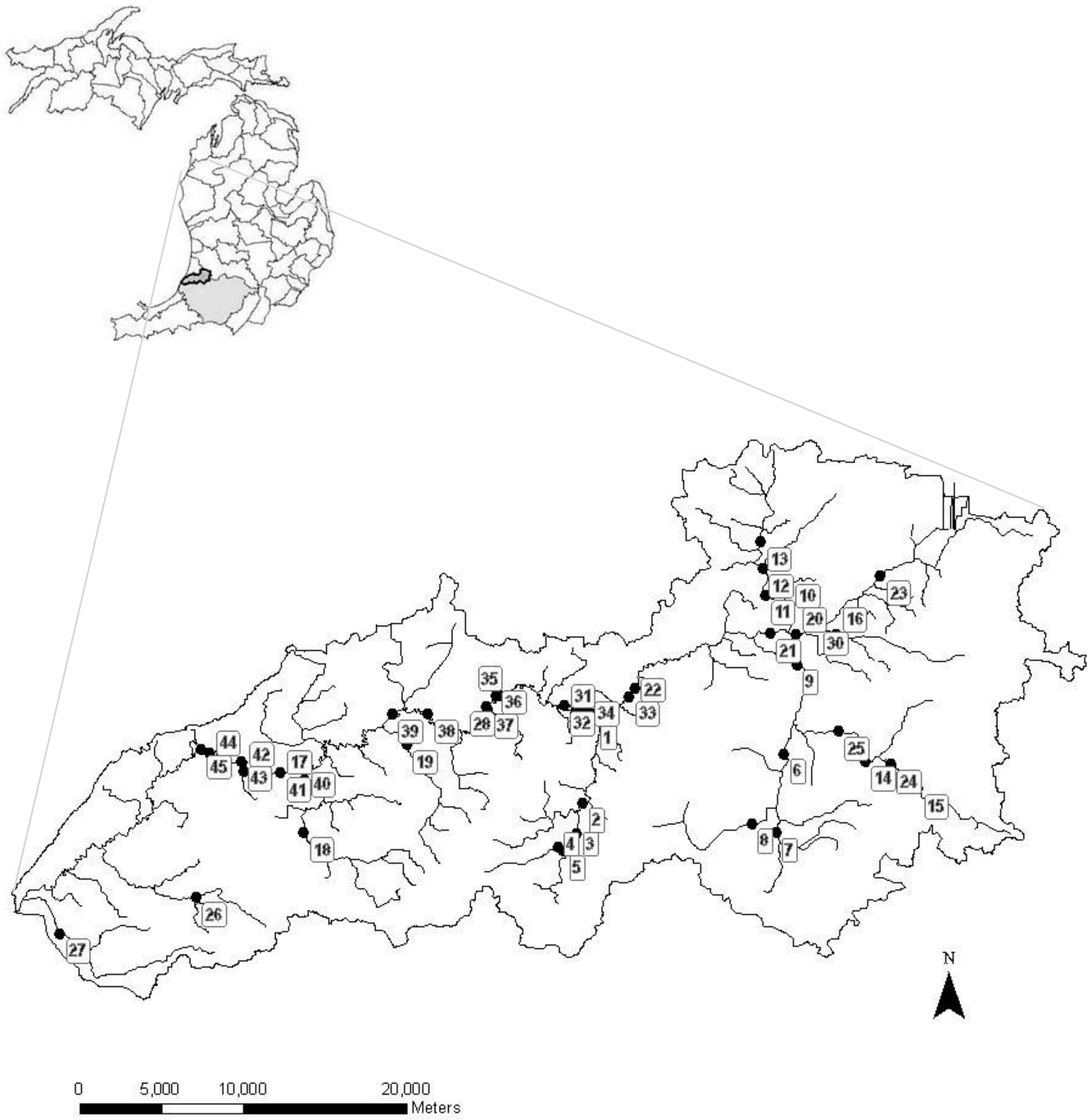


Figure 2. – Map of the Paw Paw River catchment within the St. Joseph watershed and location of 45 mussel and habitat survey sites.

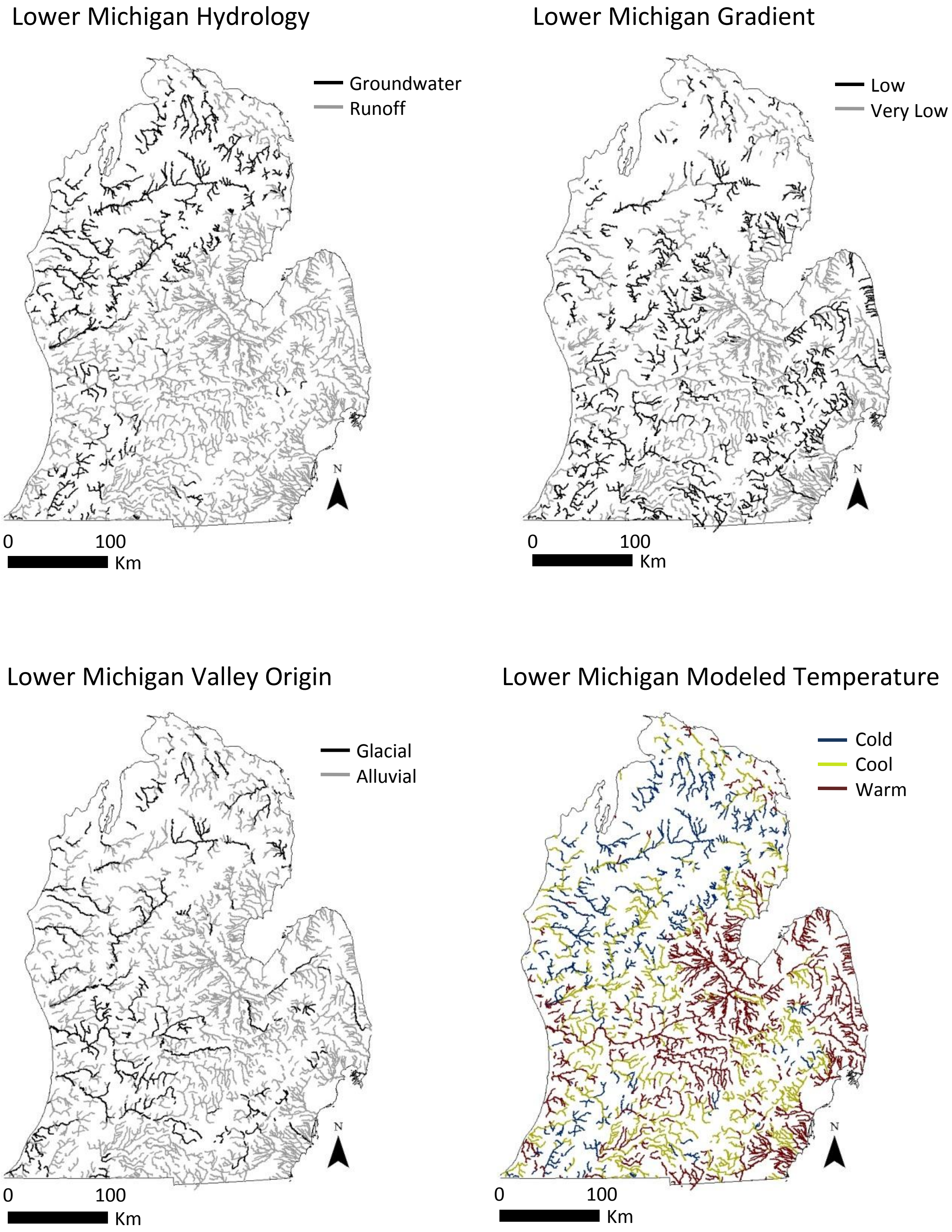


Figure 3. – Maps of Lower Michigan hydrology, gradient, valley origin, and modeled temperatures according to the MI-VSECs (Seelbach and Wiley 1997) used as predictors of unionid presence in this study.

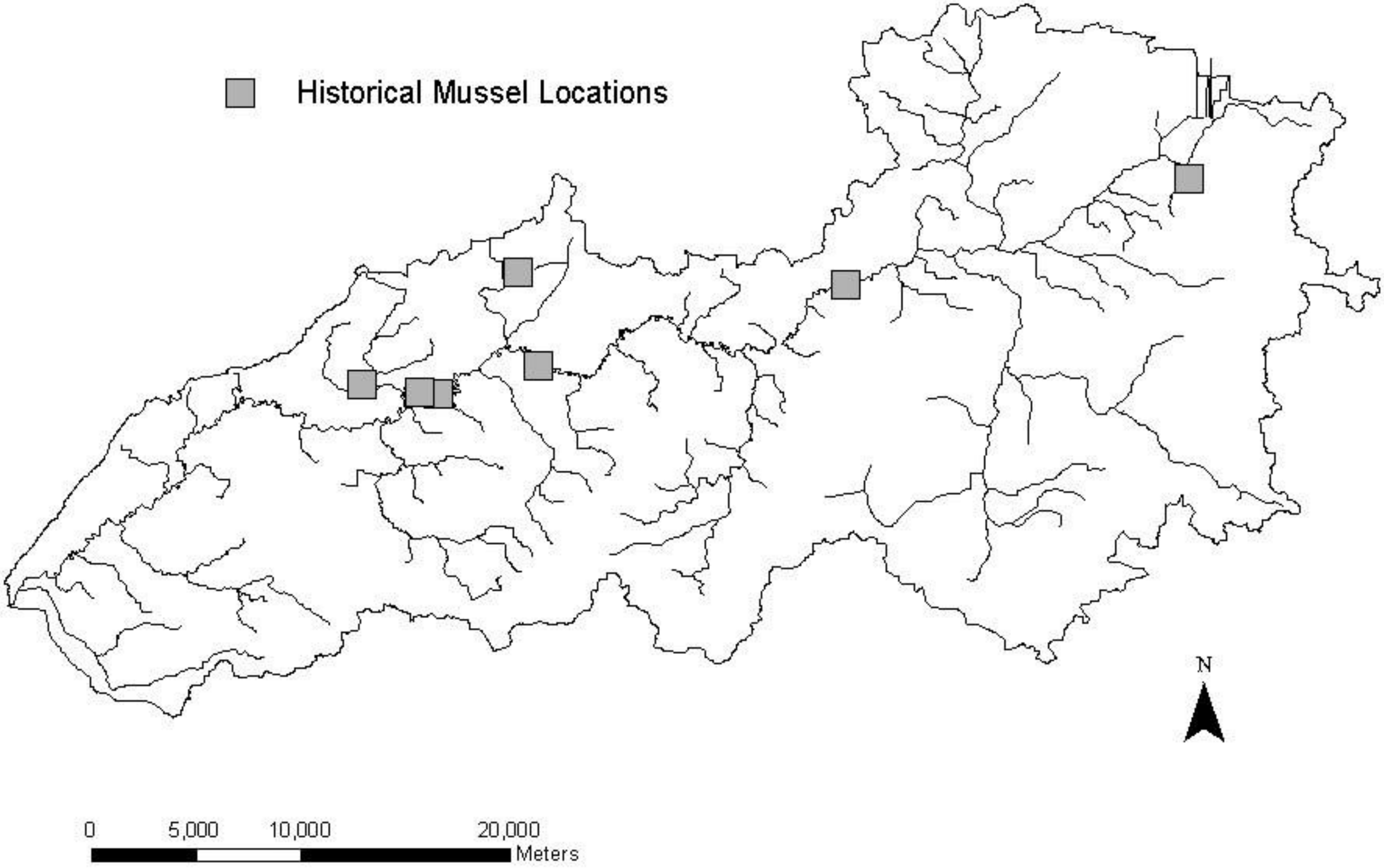


Figure 4. – Location of historical mussel sites on the Paw Paw River based on the University of Michigan Museum of Zoology collection used in this study.

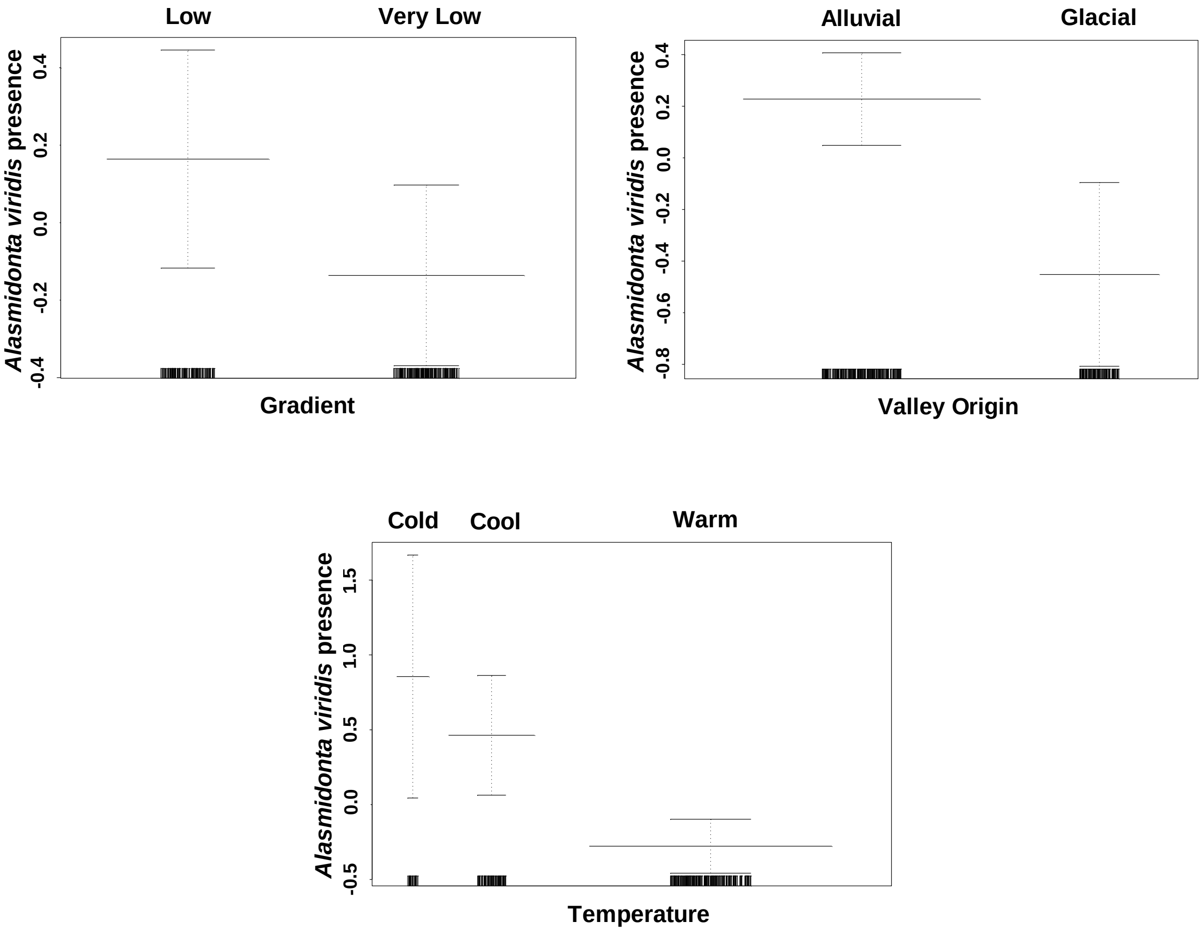


Figure 5. – Fitted probability of presence of *Alasmidonta viridis* in Michigan's Lower Peninsula from a binomial generalized linear model where presence was a function of hydrology, gradient, valley origin, and modeled temperature. Gradient, valley origin, and temperature, shown here, were significant ($p<0.05$) predictors of *Alasmidonta viridis* presence. The Y axis is standardized so zero represents mean probability of finding an individual. Bar widths represent number of data points within that variable level. Brackets represent the 95% confidence envelopes.

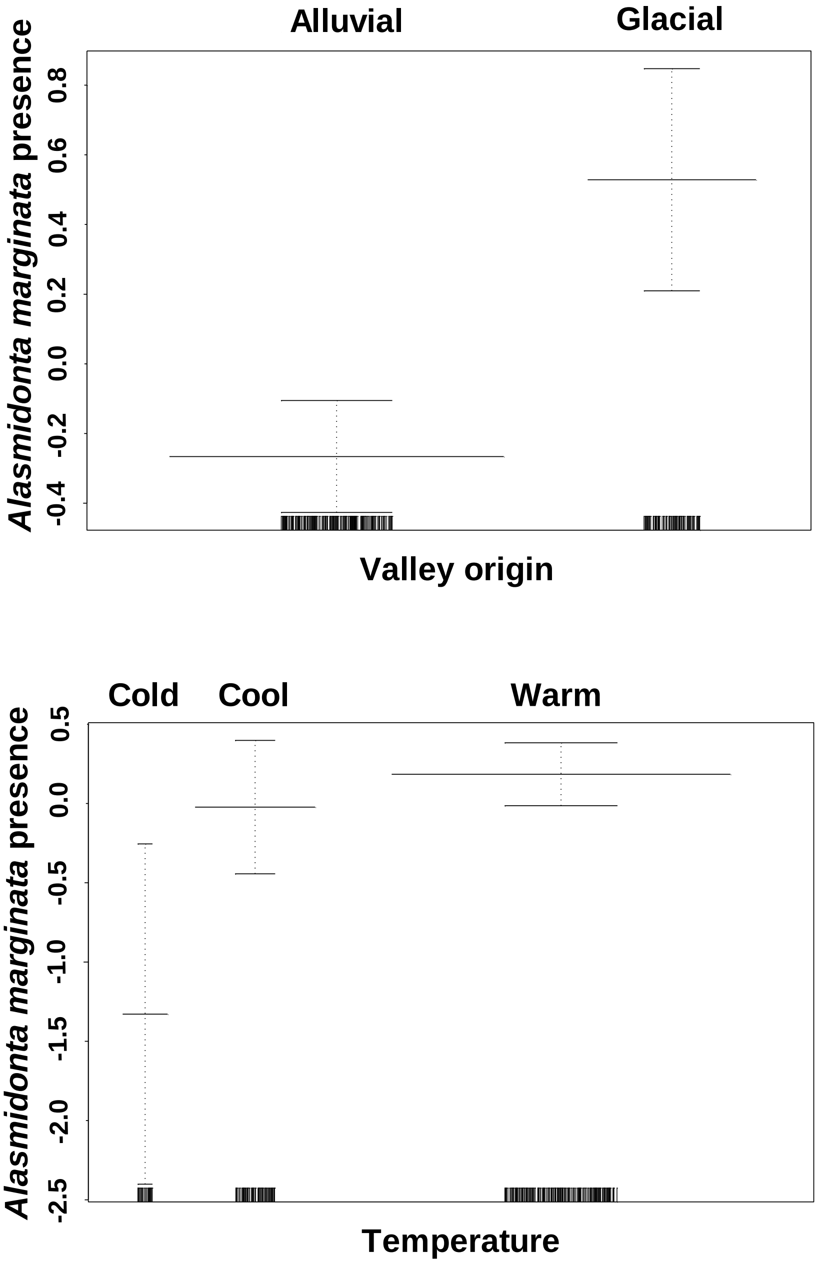


Figure 6. – Fitted probability of presence of *Alasmidonta marginata* in Michigan's Lower Peninsula from a binomial generalized linear model where presence was a function of hydrology, gradient, valley origin, and modeled temperature. Valley origin, and temperature, shown here, were significant (p<0.05) predictors of *Alasmidonta marginata* presence. Refer to Figure 5 for figure descriptions.

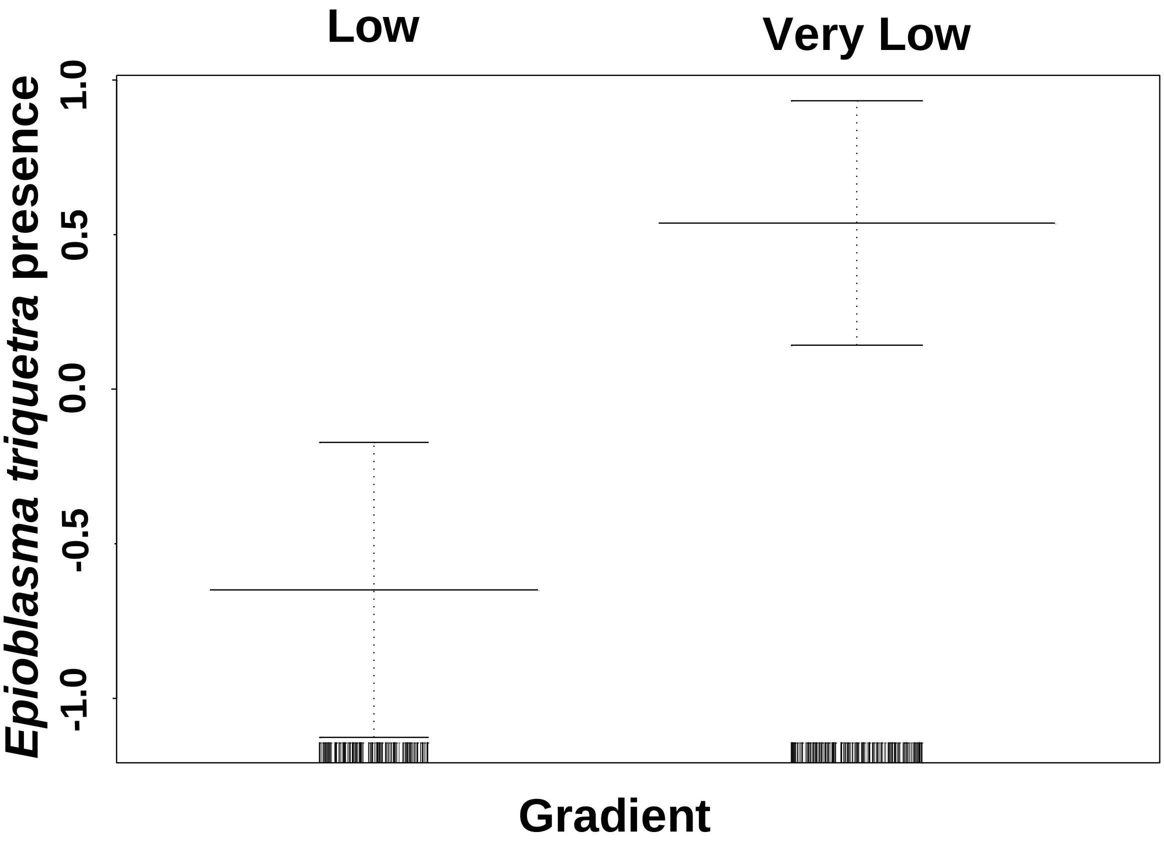


Figure 7. – Fitted probability of presence of *Epioblasma triquetra* in Michigan's Lower Peninsula from a binomial generalized linear model where presence was a function of hydrology, gradient, valley origin, and modeled temperature. Gradient, shown here, was a significant (p<0.05) predictor of *Epioblasma triquetra* presence. Refer to Figure 5 for figure descriptions.

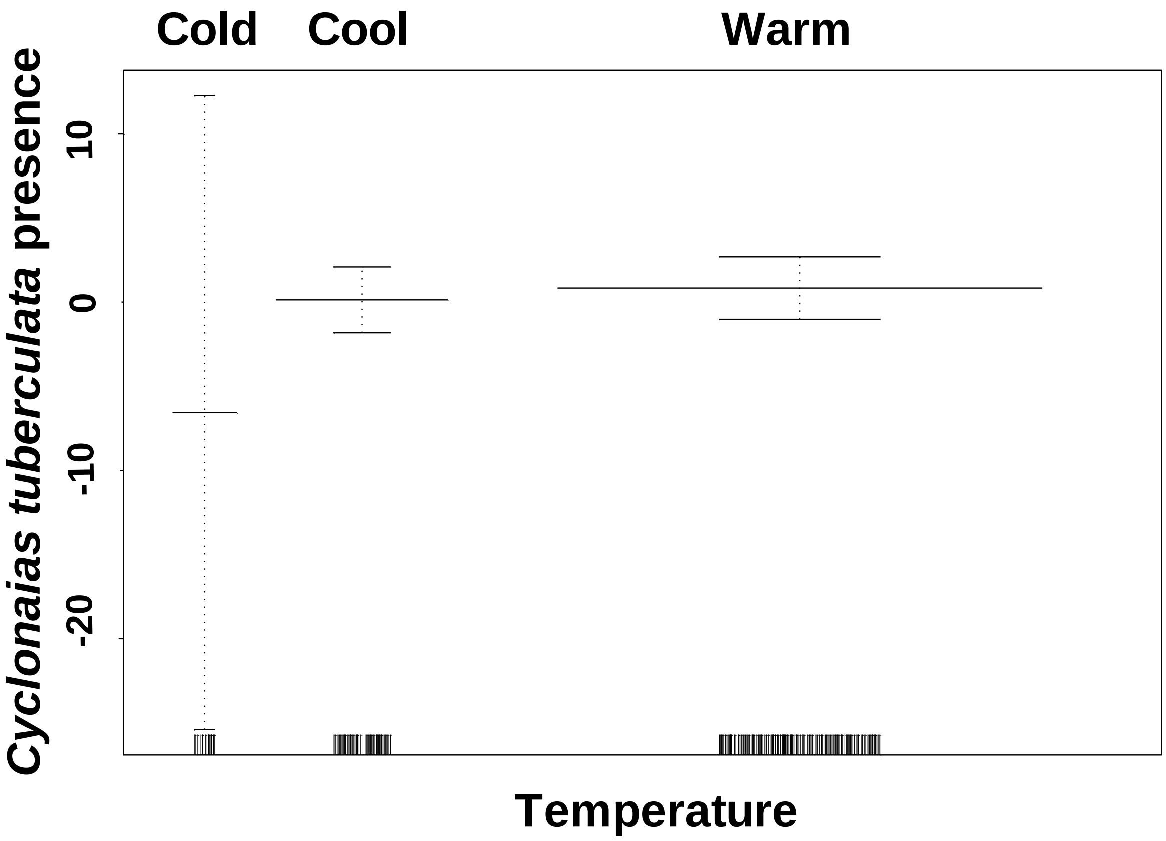


Figure 8. – Fitted probability of presence of *Cyclonaias tuberculata* in Michigan's Lower Peninsula from a binomial generalized linear model where presence was a function of hydrology, gradient, valley origin, and modeled temperature. Temperature, shown here, was a significant ($p<0.05$) predictor of *Cyclonaias tuberculata* presence. Refer to Figure 5 for figure descriptions.

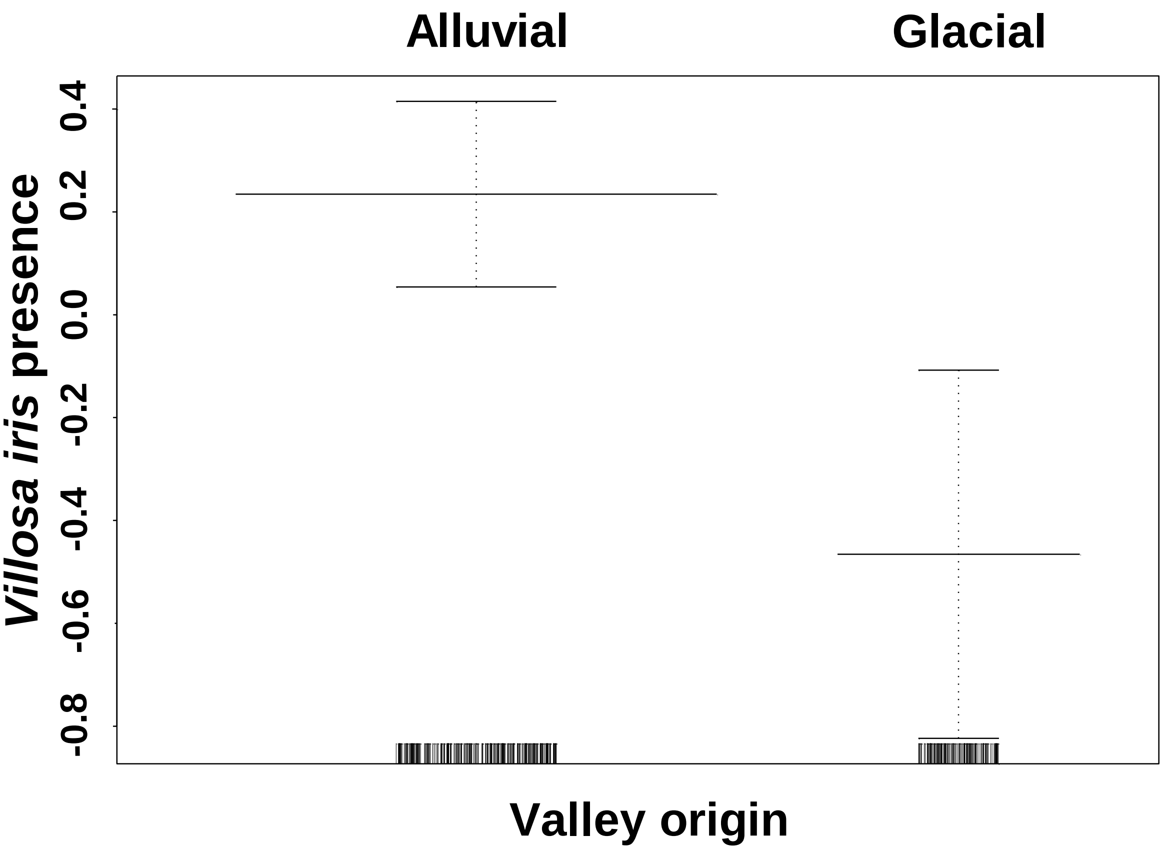


Figure 9. – Fitted probability of presence of *Villosa iris* in Michigan's Lower Peninsula from a binomial generalized linear model where presence was a function of hydrology, gradient, valley origin, and modeled temperature. Valley origin, shown here, was a significant ($p<0.05$) predictor of *Villosa iris* presence. Refer to Figure 5 for figure descriptions.

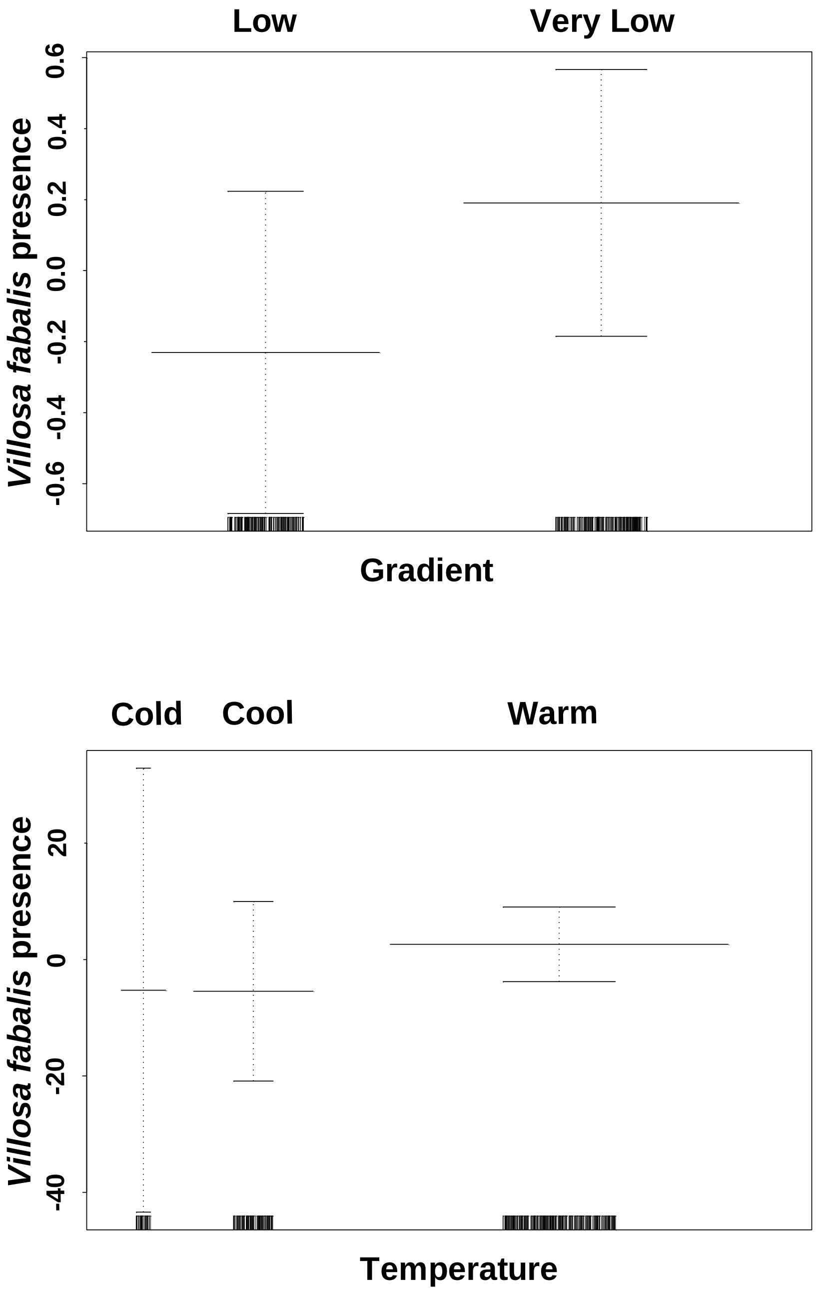


Figure 10. – Fitted probability of presence of *Villosa fabalis* in Michigan's Lower Peninsula from a binomial generalized linear model where presence was a function of hydrology, gradient, valley origin, and modeled temperature. Gradient and temperature, shown here, were significant ($p<0.05$) predictors of *Villosa fabalis* presence. Refer to Figure 5 for figure descriptions.

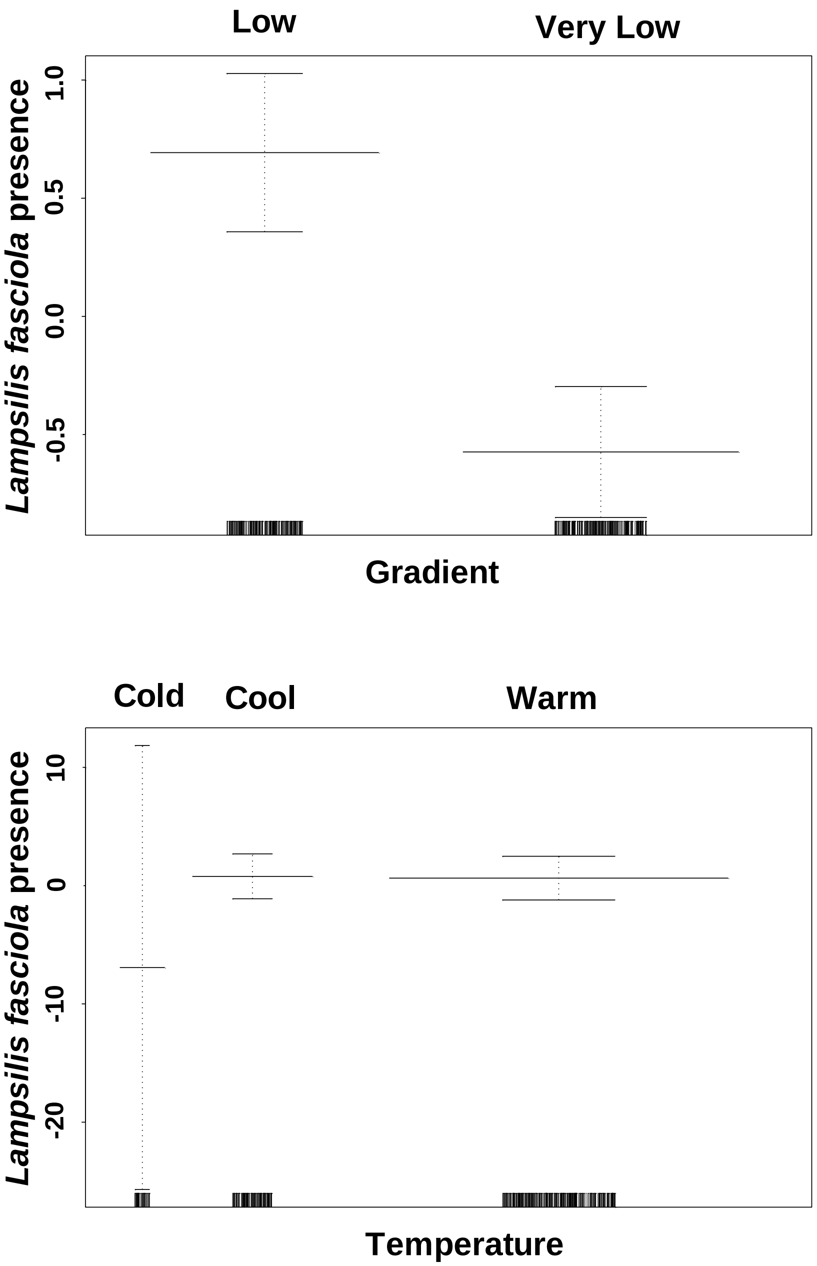


Figure 11. – Fitted probability of presence of *Lampsilis fasciola* in Michigan's Lower Peninsula from a binomial generalized linear model where presence was a function of hydrology, gradient, valley origin, and modeled temperature. Gradient and temperature, shown here, were significant ($p<0.05$) predictors of *Lampsilis fasciola* presence. Refer to Figure 5 for figure descriptions.

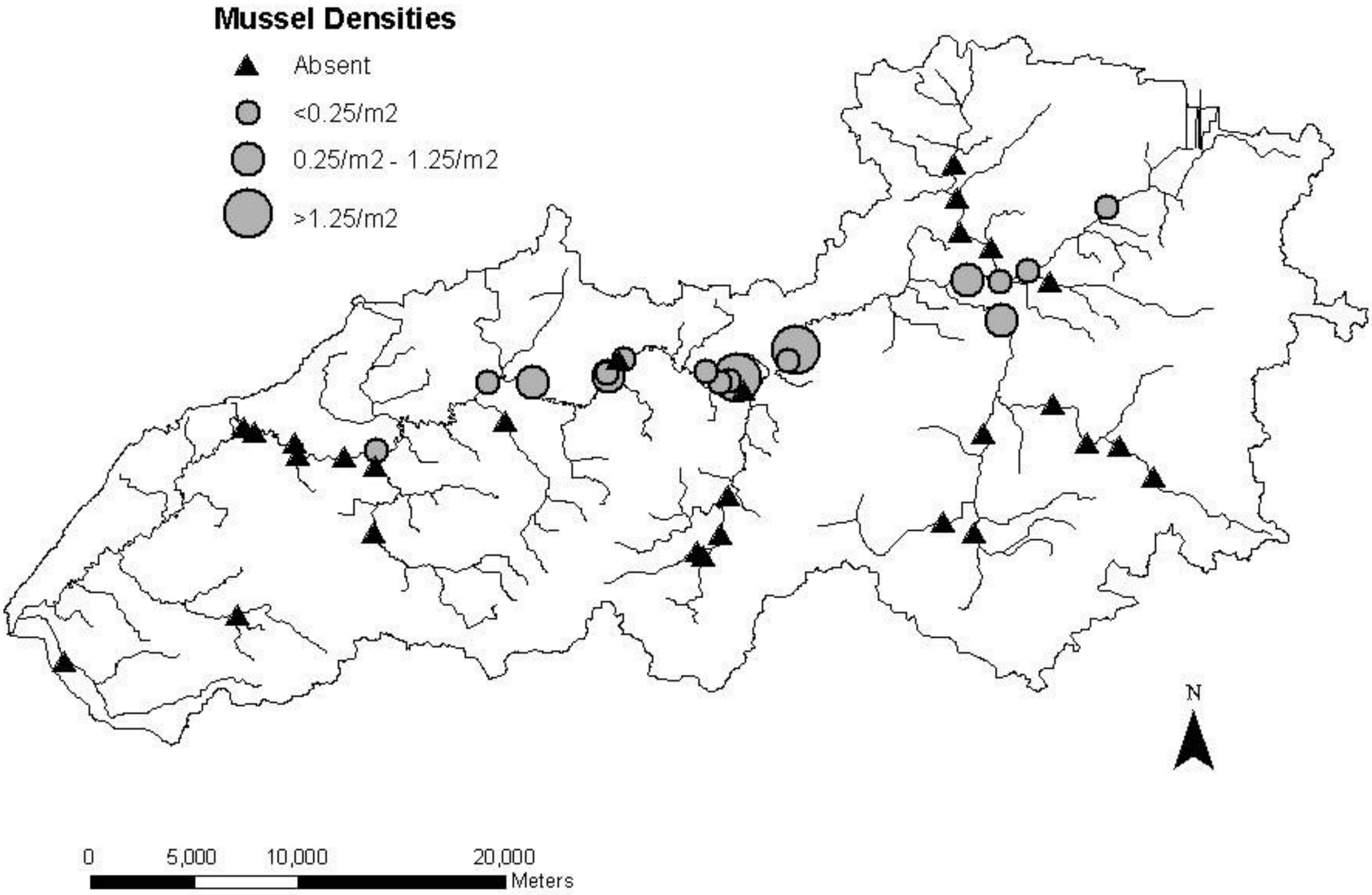


Figure 12.– Map of mussel densities in 45 sites on the Paw Paw River surveyed during the present study.

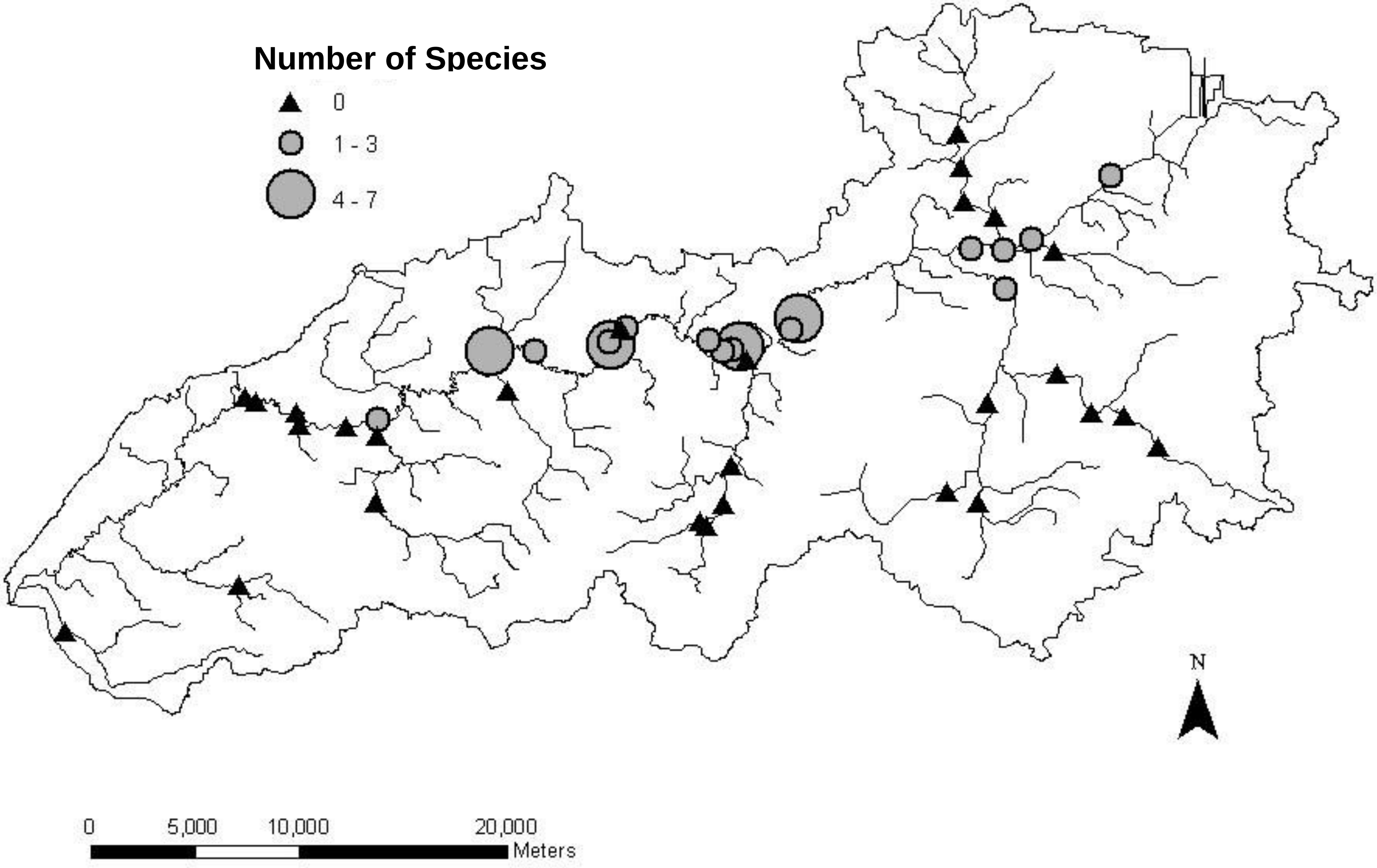


Figure 13. – Map of number of mussel species in 45 sites on the Paw Paw River surveyed during the present study.

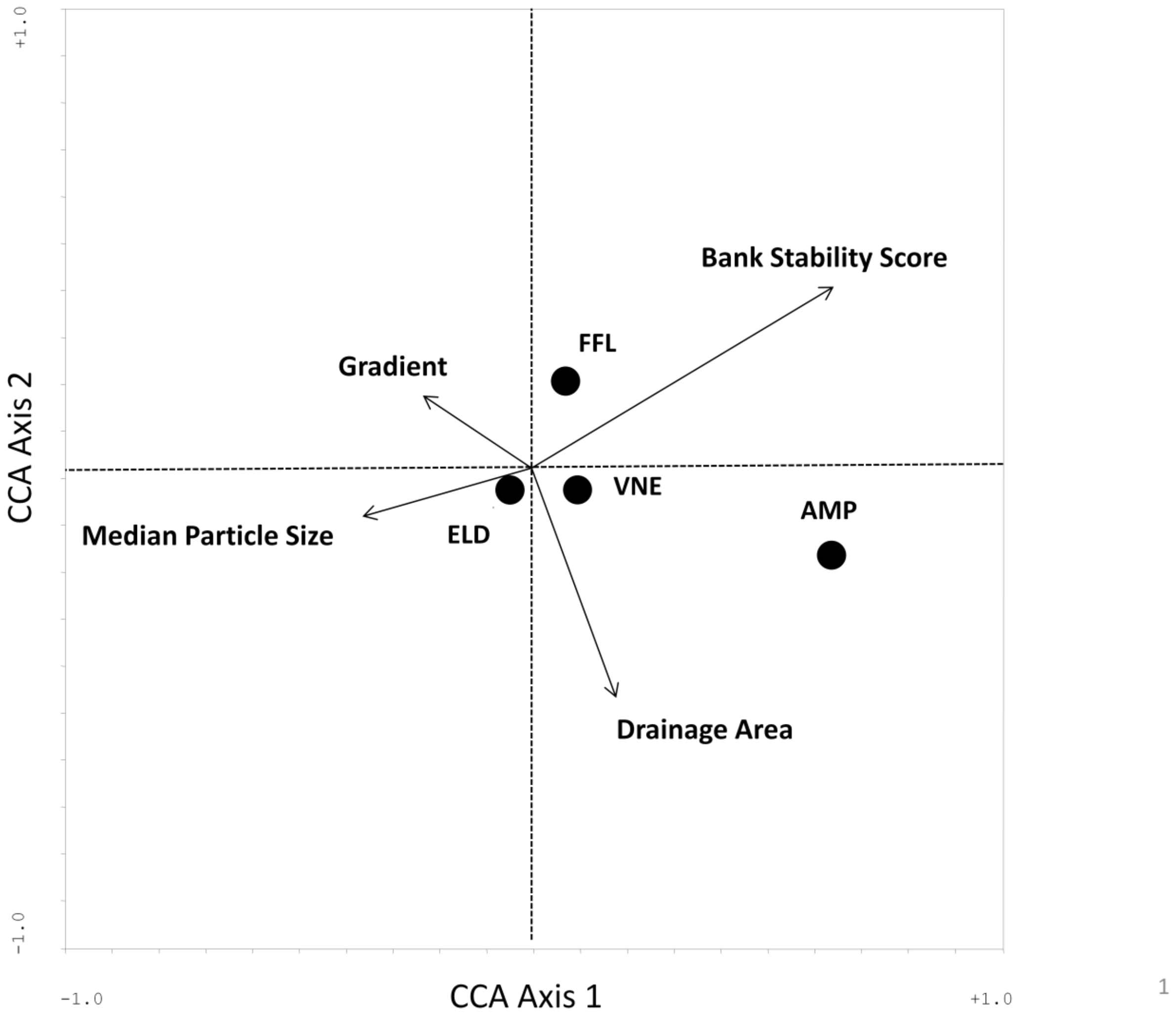


Figure 14. – Results of a Canonical Correspondence Analysis (CCA), represented as a CCA biplot for densities of the four most common species (represented as points) and environmental variables (represented as rays) in 45 sites the Paw Paw River. The length of the rays corresponds with the amount of variation explained by that variable. The perpendicular proximity of a point to a ray represents the strength of the relationship between a species and an environmental variable. The CCA indicated that bank stability score, median particle size, drainage area, and gradient explained 40% of the variation in species densities. Species abbreviations: FFL (*Fusconaia flava*), ELD (*Elliptio dilatata*), VNE (*Venustaconcha ellipsiformis*), AMP (*Amblema plicata*).

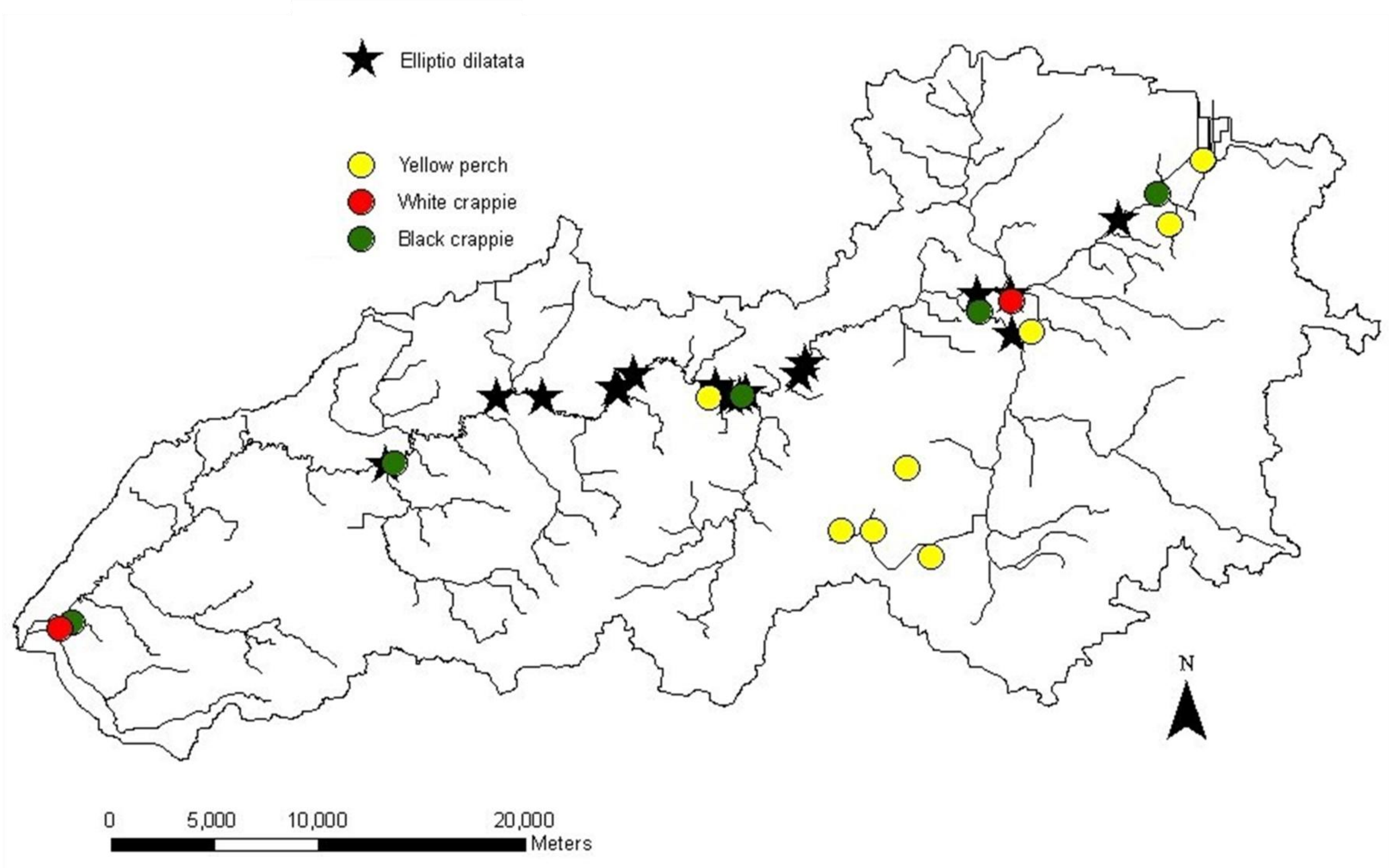


Figure 15. – Map of presence of *Elliptio dilatata* in the surveys conducted during this study and of its known host fish species in the Paw Paw River. Data points on host fish presence represent a voucher specimen (Bailey et al. 2004) and information was obtained from the Atlas of Michigan Fishes, University of Michigan Museum of Zoology.

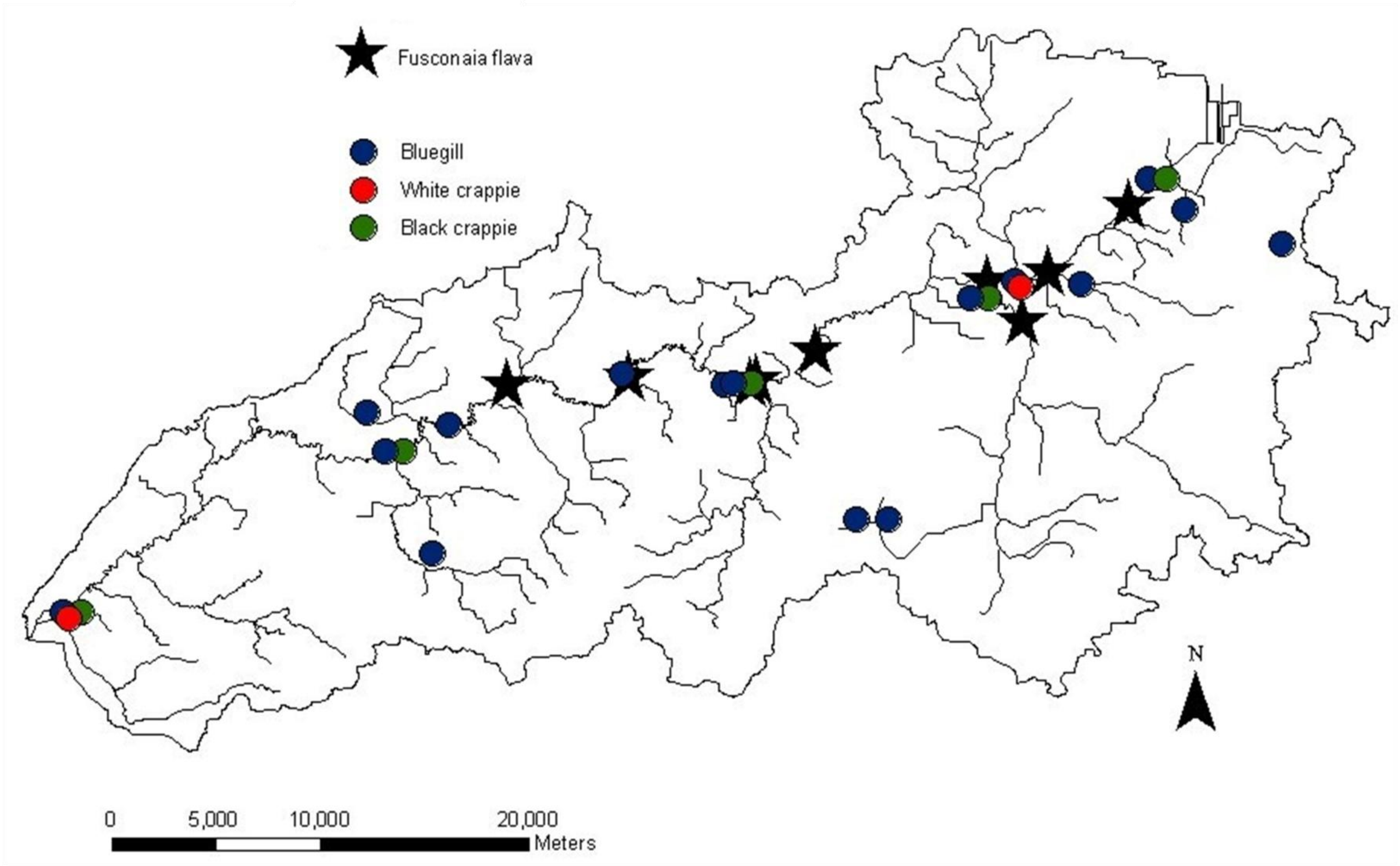


Figure 16. – Map of presence of *Fusconaia flava* in the surveys conducted during this study and of its known host fish species in the Paw Paw River. Data points on host fish presence represent a voucher specimen (Bailey et al. 2004) and information was obtained from the Atlas of Michigan Fishes, University of Michigan Museum of Zoology.

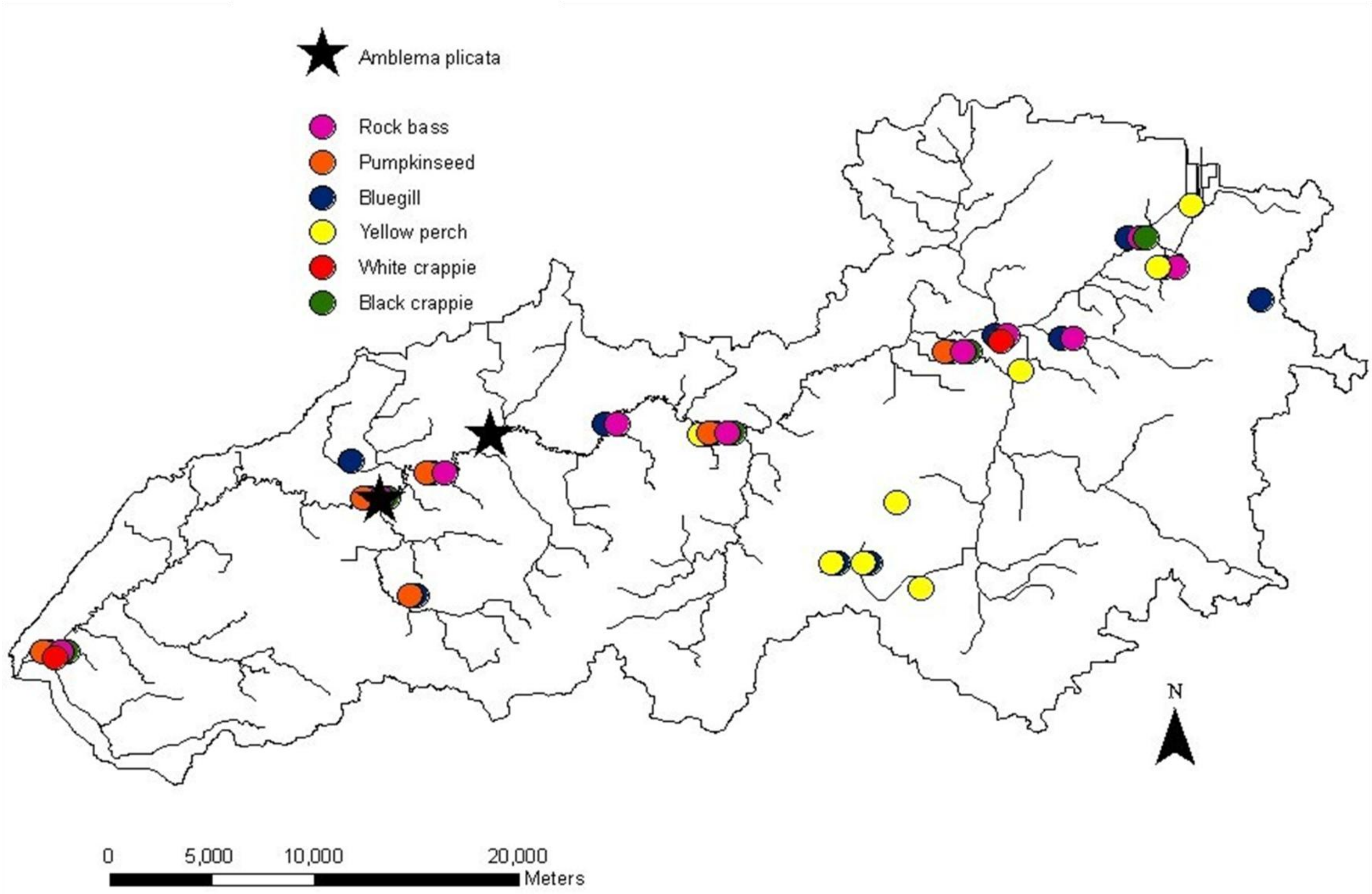


Figure 17. – Map of presence of *Amblema plicata* in the surveys conducted during this study and of its known host fish species in the Paw Paw River. Data points on host fish presence represent a voucher specimen (Bailey et al. 2004) and information was obtained from the Atlas of Michigan Fishes, University of Michigan Museum of Zoology.

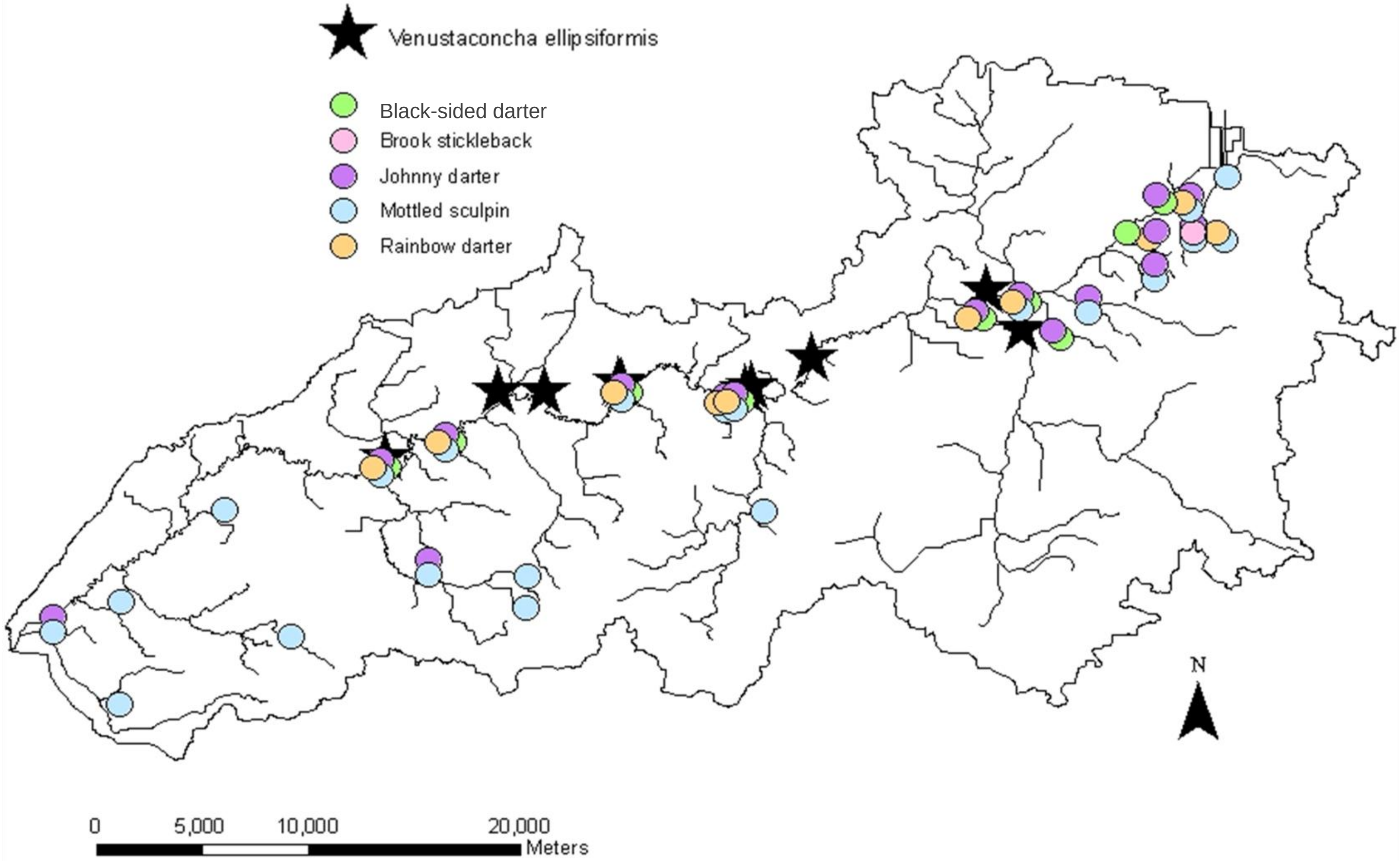


Figure 18. – Map of presence of *Venustaconcha ellipsiformis* in the surveys conducted during this study and of its known host fish species in the Paw Paw River. Data points on host fish presence represent a voucher specimen (Bailey et al. 2004) and information was obtained from the Atlas of Michigan Fishes, University of Michigan Museum of Zoology.

Chapter 2: A comparison of the distribution and habitat of unionid mussels and sea lamprey larvae in the Paw Paw River

Introduction

In the Great Lakes, invasive sea lamprey (*Petromyzon marinus*) pose serious impacts on the ecology of the region (Christie and Goddard 2003). In the adult phase, sea lamprey are parasitic on fish in the Great Lakes, particularly lake trout (*Salvelinus namaycush*). After spending 12 – 20 months in the free-swimming parasitic stage, adults migrate up into tributaries where they spawn and die. Sea lamprey larvae (ammocoetes) spend approximately 4 years or more burrowed into stream sediments feeding on detritus. Once the larval phase is complete, transformers emerge from the stream sediments and migrate downstream to the lakes where they will begin their free-swimming adult phase as fish parasites (Applegate 1950).

Treatment of tributaries harboring ammocoetes with lampricides has been the preferred method of sea lamprey control. TFM (3-trifluormethyl-4-nitrophenol) is the lethal component of lampricide (Applegate et al. 1961), and occasionally Baylucide (a molluscicide) is applied in addition to TFM to reduce the amount of TFM required on larger rivers, or to enhance TFM toxicity downstream of an application (Gilderhus 1979). Ammocoete producing tributaries are treated with lampricides about every 3 to 10 years depending on how they rank in terms of potential transformer production (Christie et al. 2003, Slade et al. 2003). According to the Great Lakes Fishery Commission, control efforts have resulted in a 90% reduction in sea lamprey populations in most areas (Dawson 2007). These chemical treatments are intended to be selectively toxic to sea lamprey, though some lethal and sub-lethal effects have been reported on other species (Gilderhus 1979, Gilderhus and Johnson 1980, US Fish and Wildlife Service Sea Lamprey Management Program 1996, Bills et al. 1992, Waller et al. 1997, Waller et al. 1998, Bogard et al. 2004, Hoggarth and Yankie 2008).

Unionid mussels may be particularly vulnerable to the nontarget effects of lampricides, and some species may be more sensitive than others (Boogard et al. 2004). The impact of lampricides on macroinvertebrates, like mussels, is not well understood. However, previous studies have observed significant sub-lethal effects of lampricides on freshwater mussels. Lampricides narcotize mussels leaving them vulnerable to beaching, predation and displacement by currents (Gilderhus 1979, Gilderhus 1980, Bills et al. 1992, Waller et al. 1997, Waller et al. 1998, Hoggarth and Yankie 2008). These narcotic effects can last up to 14 days (Waller et al. 1998). Hoggarth and Yankie (2008) found that there was an increased likelihood of beaching following TFM treatments in Conneaut Creek, Ohio. Occasionally, granular Baylucide, which is not selectively toxic, is applied in lentic environments and remains on the sediment, slowly dissolving and toxifying a thin layer of water at the sediment surface where freshwater mussels may be living (Gilderhus 1979). Gilderhus (1979) observed significant reductions in numbers of non-unionid bivalves after granular Baylucide treatments in Boardman Lake in northern Michigan, and found that 13 days after treatment all bivalves previously enumerated (105) were absent from the study area. He noted that this was not a surprising result as Baylucide is used as a molluscicide elsewhere.

In addition to employing alternative methods to control the sea lamprey population in an effort to reduce the use of chemical treatments, the Great Lakes Fishery Commission has, in the past, made modifications to lampricide treatments to minimize effects to nontarget species (McLaughlin et al. 2003). For example, juvenile lake sturgeon (*Acipenser fulvescens*), listed as endangered, threatened, or of special concern in Great Lakes states, have low tolerance to TFM (Boogard et al. 2003). As a result, tributaries where both sea lamprey larvae and lake sturgeon exist were treated later in the season, when the juvenile sturgeon were larger, and with lower concentrations of lampricide (Johnson et al. 1999). There is also concern over the sensitivity of mudpuppies (*Necturus maculosus*) to TFM exposure. In response, Ohio tributaries have been treated with lower concentrations of lampricide (Christie 2000). To date, no modifications to lampricide treatments have been made to minimize negative effects to unionid mussels.

A comparison of habitat preferences and distribution of ammocoetes and nontarget species, like freshwater mussels, is needed to determine the potential to refine lampricide treatments while still achieving the benefits of sea lamprey control. Both sea lamprey larvae and freshwater mussels are benthic riverine organisms that require substrate stability and a regular supply of food. Ammocoetes feed on detritus and are most often found burrowed in depositional areas of slow currents with soft sediments of sand and fine organic matter (Slade et al. 2003). Freshwater mussels filter feed and as a group have a wide range of habitat preferences and distributions. Most species are commonly associated with substrates of sand and gravel mixes, or sand, gravel and pebble mixes with moderate currents (Huehner 1987, Hart 1995, Badra and Goforth 2003, McRae et al. 2004). A small number of mussel species, such as *Pyganodon grandis*, are often found in depositional areas, thus habitat similar to that of ammocoetes (Huehner 1987, Hart 1995).

In this study, the overlap in distribution of ammocoetes and unionids was investigated in the Paw Paw River in southwestern Michigan, and thus the potential to refine control methods and minimize negative lampricide effects on unionid mussels. It was hypothesized that ammocoetes and unionid mussel species in the Paw Paw River have different distributions and habitat requirements. In Chapter 1, I explored the relationship between habitat and unionid species distributions on a regional-scale (Lower Michigan) using a regression approach. At the local-scale (Paw Paw River), I explored the differences in habitat use of four unionid species using species densities and a non-parametric approach, namely a canonical correspondence analysis. In this chapter the objectives were to: a) further investigate unionid mussel distribution at the local-scale based on mussel presence as a function of habitat variables in the Paw Paw River using a regression approach, b) investigate ammocoete distribution, also based on presence, as a function of habitat variables in the Paw Paw River using a regression approach, and c) compare distributions and habitat requirements of unionid mussel species and ammocoetes in the Paw Paw River.

Materials and Methods

The Paw Paw River, selected as a case study for this analysis, and the survey methods for mussel distributions were described in detail in Chapter 1. Unionid mussels were surveyed in 45 sites between June and October 2009 (Chapter 1, Fig. 2). From the 9 unionid species found live, the four most common species – *Elliptio dilatata, Fusconaia flava, Venustaconcha ellipsiformis,* and *Amblema plicata* – were selected for further analysis as remaining species were found at less than 4% of the total sites and at low densities less than 0.03/m^2.

Data on larval sea lamprey densities and habitat for the Paw Paw River were from databases available from the Great Lakes Fisheries Commission (GLFC) and the U. S. Fish and Wildlife Service (USFWS). Databases contain historical records from Quantitative Assessment Surveys (QAS), used in the Empirical System Treatment Ranking (ESTR), and from distribution surveys conducted by the USFWS. QAS data selected for the analysis were collected during spring and summer in 1999, 2000, and 2004 at 75 access sites (Fig. 19).

The QAS collected habitat data, based on substrate as relevant to ammocoetes and sea lamprey spawning, and larval density data. At each of the 75 access sites, substrate was measured along four transects, and the length of type I, type II, or type III habitat, and spawning habitat were recorded (Slade et al. 2003). Type I is the preferred ammocoete habitat, generally located in depositional areas and composed mostly of sand and fine organic matter. Type II is composed of mostly sand and may include some gravel. Both types I and II are suitable for lamprey larvae but type I is the preferred habitat and densities are higher than in type II habitat (Slade et al. 2003). Type III is not suitable for ammocoetes. It can be composed of hardpan clay, densely packed gravel, or bedrock; substrates that ammocoetes cannot burrow into (Slade et al. 2003). At each site, ammocoetes were sampled using an electrofisher in two 15m^2 plots placed in habitat type I. Ammocoetes were also surveyed in two 15 m^2 plots in habitat type II in selected sites. Larvae data from type II habitat were excluded from the analysis as plots in type II habitat were scarce. Ammocoetes were collected and indentified to the species level (several species of native lamprey are also found in Michigan streams), counted, and measured (Slade et al. 2003).

Ammocoete length measurements were used to group them into age categories. Following Adlerstein and Silverman (2008) and based on typical length frequency distribution of ammocoetes, small ammocoetes <50mm were taken to represent young-of-the-year, medium ammocoetes 50 – 100mm to represent larvae age one, and large ammocoetes >100mm to represent older larvae including transformers. Young-of-the-year larvae were too small to be well assessed with an electrofisher and densities in the surveys were under-represented.

The USFWS organizes sea lamprey surveys and control treatments based on non-overlapping "stream reaches" (Anonymous 2001). Each reach in sea lamprey producing systems is periodically surveyed by QAS for ammocoetes, and the number of ammocoetes potentially leaving the system as transformers per reach is calculated to rank reaches for treatment. Reaches that rank high are subsequently treated with lampricide, so not all reaches in a system are necessarily treated within the same year. The Paw Paw River was divided into five reaches; Reach 4 is the mainstem, and Reaches 5, 6, 7 and 8 were the larger tributaries (Fig. 20). Treatment schedules for the Paw Paw River were provided by the USFWS (Table 6). Larval data from surveys done two or more years after treatment were used in the analysis, as it takes a couple of years after treatment to find ammocoetes in streams (Adlerstein and Silverman 2008).

Local habitat variables measured during this study and included in this analysis were median particle size and bank stability score. Median particle size was calculated from visual estimations of substrate composition and bank stability score was measured as a component of the Qualitative Habitat Evaluation Index (QHEI) described in detail in Chapter 1. Median particle size ranged from 0.0625 to 9mm. Sites were scored on a scale from 1 to 3 for bank stability. A score of 1 represented severely eroded, unstable banks. A score of 2 represented some erosion and moderately stable banks. A score of 3 represented little or no erosion and stable banks. No sites scored 1; therefore bank stability had two levels – moderately stable and stable.

Landscape habitat variables for this analysis - gradient (m/km), drainage area (km^2), and hydrology classification were available from the Michigan Department of Natural Resources Landscape-Based Ecological Classification System for River Valley Segment Classification (MI-VSEC) database. Gradient in the Paw Paw River ranged from 0.04 to 4.36m/km and drainage area from 15.83 to 707.24 km^2. The hydrology VSEC classification was re-scaled from its original nine levels into two levels – groundwater-driven and runoff-driven as described in Chapter 1 (Table 1).

Another variable considered in the analysis was the distance to sea lamprey spawning habitat found in sites upstream. Distance to sea lamprey spawning habitat has been shown to be a significant determinant of ammocoete distribution in Michigan Lower Peninsula streams (Adlerstein and Silverman 2008). Sea lamprey spawning habitat consists of substrate larger than 9mm in diameter with some sand and flow velocities between 0.5 to 1.5 m/s (Anonymous 2001). Distance to spawning habitat was calculated by determining the distance of each sampling plot to the nearest upstream location were spawning habitat was recorded during QAS and other historical surveys. Additional data on distribution of spawning habitat based on substrate size composition data was acquired during habitat surveys done between June and October 2009 on the Paw Paw River (Chapter 1). If a site consisted of 10% or more gravel substrate (2 – 16mm) or larger, it was considered suitable sea lamprey spawning habitat. River distance was calculated using ArcMap v. 9.3.1 (ESRI 2009). Distance to spawning habitat in the Paw Paw River ranged from 0 to 25,851m.

The relationships of ammocoete and unionid distributions and habitat in the Paw Paw River were investigated using a modern regression approach. The distributions based on presence of the four most common unionid species (*Elliptio dilatata, Fusconaia flava, Venustaconcha ellipsiformis,* and *Amblema plicata*), and of medium, large, and total ammocoetes were included in the analysis. Small ammocoetes were not modeled separately as they were found in less than 4% of plots sampled. For the analysis, generalized additive models (GAM) (Hastie and Tibshirani 1990) and generalized linear models (GLM) (McCullagh and Nelder 1989) were used. First, GAMs were used to explore the shape of the relationships between the response variables and covariate predictors incorporated as smooth terms. Then GLMs were implemented and polynomial terms were used to represent non-linear relationships when necessary. Routines available in the S-PLUS computing environment gam() and glm() were used to conduct the analysis (TIBCO Software Inc 2007).

The distribution of the unionid species was modeled as a function of median particle size, gradient, and bank stability and incorporating a binomial probability distribution to relate the response and predictors using the GLM as follows:

$$g(\mu_{mdb}) = \alpha + \beta X_m + \delta X_d + \xi_b \qquad (2)$$

where g() was the logit link function $\ln[\mu_{mdb} /(1- \mu_{mdb})]$, μ was the expected probability of unionid species presence in sites with median particle size represented by *m*, gradient represented by *d,* and bank stability represented by *b.* Median particle size and gradient were introduced as covariates and bank stability was introduced as a factor with two levels.

Distribution of medium, large and total ammocoetes was modeled as a function of distance to spawning habitat *s* introduced as a non-parametric smooth covariate, and hydrology *h* and bank stability *b* introduced as factors with two levels each. Models incorporated a binomial probability distribution to relate the response and predictors using a GAM as follows:

$$g(\mu_{shb}) = \alpha + f(\lambda_s) + \delta_h + \xi_b \qquad (3)$$

where g() was the logit link function, μ was the expected probability of medium, large and total ammocoete presence. If the results of the GAM indicated that the relationship between presence of ammocoetes and the distance to spawning habitat *s* was significantly non-linear a GLM was fitted with the term introduced as a polynomial with degrees of freedom equivalent to the smooth to provide model parameters.

Distribution of medium, large and total ammocoetes was also modeled as a function of the distribution of two species of unionids - *Elliptio dilatata* and *Fusconaia flava*. *Venustaconcha ellipsiformis* and *Amblema plicata* were not included as predictors as the distribution of these species perfectly overlapped with *Elliptio dilatata* and *Fusconaia flava,* respectively. GLMs incorporated a binomial probability distribution to relate the response and predictors as follows:

$$g(\mu_{ef}) = \alpha + \lambda_e + \delta_f \qquad (4)$$

where g() was the logit link function, μ was the expected probability of the presence of medium, large and total ammocoete as a function of the presence of *Elliptio dilatata* represented by *e*, and *Fusconaia flava* represented by *f*. Both predictors were introduced as factors with two levels (presence and absence).

Results

In the Paw Paw River, live mussels were found at 17 of the 45 sites. Most sites where live individuals were found were located on the mainstem of the Paw Paw River (Fig. 21). A total of 842 live unionid mussels were counted representing 9 species. The mean density of all species combined was 0.59 individuals/m^2 at sites where live individuals were present and reached a maximum of 5.16/m^2.

The distribution of the four selected mussel species – *Elliptio dilatata, Fusconaia flava, Venustaconcha ellipsiformis, and Amblema plicata* – was significantly dependent upon one or more of the habitat variables included in the analysis: medium particle size, gradient, and bank stability (Table 7 and 8). All the species had a significant negative relationship with gradient (Fig. 22, 23, and 24). This variable also accounted for most of the explained deviance in all of the models (Table 7). *Venustaconcha ellipsiformis* displayed a significant positive relationship with median particle size (Fig. 23) and *Amblema plicata* had a significant positive relationship with bank stability (Fig. 24). Of the four models, the model for *Fusconaia flava* explained the least deviance. *Amblema plicata* had the strongest negative relationship with gradient and *Fusconaia flava* the weakest.

Sea lamprey larvae were present throughout the mainstem and tributaries of the Paw Paw River except in the South Branch and East Branch due to the existence of a dam that is impassable by adult sea lamprey. However, densities were higher in the tributaries (Fig. 21) and ranged from 0.13 individuals/m^2 to 2.4/m^2.

The distribution of medium, large and total ammocoetes was significantly dependent upon one or both of the following habitat variables: distance to spawning habitat and bank stability. Hydrology was not a significant predictor of ammocoete presence (Table 9 and 10). Medium ammocoetes had a significant negative relationship with distance to sea lamprey spawning habitat and a significant positive relationship with bank stability (Fig. 25). Large ammocoetes and total ammocoetes displayed a significant positive relationship with bank stability (Fig. 26). The model for total ammocoetes explained the most deviance (Table 9). Bank stability significantly predicted and was positively related to distribution of medium, large and total ammocoetes. This variable accounted for most of the explained deviance in the large and total ammocoete models, while distance to spawning habitat accounted for most of the explained deviance in the medium ammocoete model (Table 9). Of the three models, large ammocoetes had the strongest positive relationship with bank stability.

Ammocoete and unionid distributions overlapped minimally in the Paw Paw River. Ammocoete densities were lowest in Reach 4, the mainstem, and highest in Reach 5. Unionid mussel densities were highest in Reach 4 and unionids were absent from all other reaches (Fig. 27). *Fusconaia flava* presence was significantly and negatively related to the presence of total ammocoetes (Table 11, 12 and Fig. 28). *Elliptio dilatata* presence was not significantly related to presence of ammocoetes of any size.

Discussion

There was minimal overlap of unionid mussel and larval sea lamprey distributions of any of the three size categories in the Paw Paw River. Unionid mussels were found only in the middle and upper portions of Reach 4 (the mainstem), while ammocoete densities were highest in Reaches 5, 7, and 8 (the tributaries) and in one site in the lower portion of Reach 4. In the middle and upper portions of Reach 4, where mussels were present, ammocoetes were present in less than 30% of sites sampled and, where present, were found in low densities. These densities were also low relative to other Lake Michigan tributaries harboring larval sea lamprey and fell in the bottom 20% of the mean ammocoete density range for Lake Michigan tributaries (Adlerstein and Silverman 2008). These distributions indicated that the upper and middle portions of Reach 4 in the Paw Paw River were relatively unimportant as ammocoete producers and were particularly important to unionid mussels.

The upper and middle portions of Reach 4 were not ideal for lamprey because habitat was not stable. Bank stability, which is indicative of flow stability, was a significant predictor of medium, large and total ammocoete presence. The majority of Reach 4 was runoff driven which causes flows to be less stable and can scour out the fine organic matter that is a component of preferred substrate of ammocoetes (Seelbach et al. 1997, Slade et al. 2003). These flashier flows in Reach 4 could also have pushed ammocoetes further away from spawning sites, downstream to sites where there was more stable habitat of slower currents and finer substrate. Indeed, ammocoetes in this system were found in highest densities in the lower portion of Reach 4 rather than close to spawning habitat. It is likely that with time, ammocoetes grow in size, and flashy flows in Reach 4 push them downstream, causing larger lamprey to be found at sites at increasing distances from spawning habitat. These results are consistent with Adlerstein and Silverman's (2008) findings from a similar analysis including slightly different predictors. Additionally, Reach 4 sites had substrate dominated by flowing sand (>80% diameter = 0.00625 – 2mm) or sand, gravel (2 – 16mm), and pebble (16 – 64mm) mixes – not an ideal habitat for ammocoetes.

Although not ideal for sea lamprey larvae, the upper and middle portion of Reach 4 contained suitable habitat for unionid mussels. Though the four most common species in the Paw Paw River had some differences among their habitat preferences, this range was mostly outside that of ammocoete habitat. For example, model results indicated that presence of all species were positively associated with increased bank stability, although only in the case of *Amblema plicata* the relationship was significant, which is consistent with previous analysis indicating that mussels require some level of hydrologic stability (Strayer 1999, McRae et al. 2004, Strayer 2008). However, mussels were able to persist in areas where flow was too unstable for ammocoetes as was the case in the upper and middle portion of Reach 4 where flow stability fell within the range for mussels, but not ammocoetes. Mussels have more mass than larval sea lamprey, and therefore, may be more tolerant of slightly unstable flows that can cause scouring.

The substrate composition in the upper and middle portion of Reach 4 was suitable for unionid mussels. The presence of all four of the most common species in the Paw Paw River was positively associated with increases in median particle size in the models, and the relationship was significant for *Venustaconcha ellipsiformis*. These results are consistent with the findings of previous studies which indicated that *Amblema plicata* and *Fusconaia flava* preferred sand and gravel mixes (Hart 1995, McRae et al. 2004, Chapter 1) and *Venustaconcha ellipsiformis* and *Elliptio dilatata* preferred sand gravel and pebble mixes (Huehner 1987).

Lastly, Reach 4 had suitable gradient for unionid mussels. The presence of the four most common mussel species was significantly predicted by decreases in gradient. In a study done in the northern Atlantic Slope, Strayer (1993) also found gradient to significantly predict the presence of some unionid species; though gradient in Lower Michigan streams is far lower than gradient in streams of the northern Atlantic Slope. The gradient in the Paw Paw River ranged from 0.04 - 4.4m/km. The survey sites in the middle and upper portions of Reach 4, where unionid mussels were found, had gradients at the lower end of this range; less than 0.6 m/km and less than 1.4 m/km, respectively.

The presence of total ammocoetes in the Paw Paw River was a significantly associated with the absence of *Fusconaia flava*. Future sea lamprey surveys could benefit from incorporating this knowledge into survey methods. Also, surveys could benefit from further information on overlap in distribution of sea lamprey larvae and unionid mussel species. A more comprehensive database and understanding of unionid mussel distributions could be gained by collecting information on the presence of unionid species during the larval sea lamprey surveys, as these surveys occur throughout tributaries in the Great Lakes.

The Paw Paw River contained relatively low ammocoete densities (Adlerstein and Silverman 2008) and the number of transformers it produced yearly was well below that of most Lake Michigan tributaries; this makes it a good candidate for lampricide treatment modifications (McLaughlin et al. 2003). These modifications would only be necessary in Reach

4, as the nontarget species of interest, unionid mussels, were only present in this reach. Reach 4 was the largest reach and densities of ammocoetes within the reach were variable: historical surveys have yielded mean estimates of 0.01 ammocoetes/m^2 in the upper portion, 0.04 ammocoetes/m^2 in the middle portion, and 0.1 ammocoetes/m^2 in the lower portion. Thus, the upper and middle portions - where unionid mussels were present - have the lowest mean ammocoetes densities in the Paw Paw River. Segmenting Reach 4 into smaller reaches – upper, middle, and lower (Fig. 29) – and avoiding treating those segments where mussels are abundant is one possibility for refining treatment. Reach 4, has been treated frequently, potentially harming the unionids located in the area. Segmenting Reach 4 so that only areas with high ammocoete densities and low unionid densities would be treated could result in reducing treatment costs and minimizing threats to unionid conservation while still controlling the sea lamprey contribution to Lake Michigan.

Spatial definition of sea lamprey and unionid surveys can influence results in this study. Ammocoete surveys were conducted at a smaller scale than the unionid surveys. Ammocoetes were sampled within 15m^2 plots (Slade et al. 2003), while unionids surveys were conducted within 120m^2 plots. Additionally, ammocoetes were not sampled at random but were conducted in locations where ammocoete presence is most likely (habitat type I in this study), (Slade et al. 2003). This can explain the small variation in ammocoete presence among sites in the Paw Paw River (reduced null deviance in the generalized linear models). This non-random sampling reduces the opportunities to find contrast in other habitat variables that would predict ammocoete distribution.

Ideally, the benefits of sea lamprey control should not come at the cost of impacting nontarget species, particularly threatened taxa such as unionids, and decreasing biodiversity. Results from this study indicated that with a better understanding of ammocoete and nontarget species distribution overlap and a comparison of habitat preferences, sea lamprey control in the Great Lakes can be achieved with minimal impacts to nontarget species and biodiversity. Further comparative analysis of ammocoete and unionid distributions at the Michigan regional-scale would be most valuable to understand differences in habitat requirements of these benthic organisms. Unfortunately, an analysis at the regional-level is currently not practical as a Michigan state-wide database of historical and current mussel species distributions is unavailable. Incorporating additional tasks of recording presence of unionid species during QAS and distribution surveys for sea lamprey larvae, which should come at not additional cost, would help further in understanding the overlap in distributions and refining lampricide treatments with benefits for sea lamprey control and unionid conservation.

Table 6. – Lampricide treatment schedule for the Paw Paw River by reach. Treatment data were made available by the US Fish and Wildlife Service.

Treatment year	Reach 4	Reach 5	Reach 6	Reach 7	Reach 8
1981	x				x
1985		x	x	x	x
1988	x	x		x	x
1992	x	x	x	x	
1997	x	x	x	x	
2001	x	x	x		x
2005	x	x			
2009	x	x	x	x	x

Table 7. – Analysis of deviance for binomial generalized linear models for presence of *Elliptio dilatata, Fusconaia flava, Venustaconcha ellipsiformis, and Amblema plicata* in the Paw Paw River as a function of median particle size, gradient, and bank stability. Median particle size and gradient were introduced as covariates. Bank stability was a factor with two levels (moderately stable, stable). * indicates that the variable is significant at the p<0.05 level.

			Percent deviance explained by variables			
Unionid Species	**Proportion of sites present**	**Null deviance**	**Total**	**Median particle size**	**Gradient**	**Bank stability**
Elliptio dilatata	0.36	57.68	36.27%	4.65%	*31.25%	0.38%
Fusconaia flava	0.20	44.58	20.41%	4.40%	*15.58%	0.43%
Venustaconcha ellipsiformis	0.22	47.16	49.88%	*17.22%	*32.6%	0.05%
Amblema plicata	0.05	16.27	57.32%	0.39%	*25.5%	*31.43%

Table 8. – Coefficients for binomial generalized linear models for presence of *Elliptio dilatata, Fusconaia flava, Venustaconcha ellipsiformis,* and *Amblema plicata* in the Paw Paw River as a function of median particle size, gradient, and bank stability. Coefficients are on the logit scale. Median particle size and gradient were introduced as covariates. Bank stability was a factor with two levels (moderately stable, stable) where the coefficients represented the difference with the first level included within the intercept. * indicates that the slope of the covariates are significantly different than 0 and that distribution of the selected species in stable banks is significantly different to that in moderately stable banks at the p<0.05 level.

Unionid Species	Intercept	t value	Median particle size	t value	Gradient	t value	Bank stability	t value
Elliptio dilatata	0.576	0.756	0.407	2.126	*-0.432	-2.973	0.390	0.467
Fusconaia flava	-0.859	-1.111	0.275	1.809	*-0.277	-2.016	0.371	0.437
Venustaconcha ellipsiformis	-0.610	-0.703	*0.770	2.586	*-0.622	-2.316	0.167	0.158
Amblema plicata	-13.09	-0.260	0.78	1.096	*-1.34	-1.189	*12.53	0.249

Table 9. – (*a*) Analysis of deviance for binomial generalized linear models for presence medium, large, and total ammocoetes in the Paw Paw River as a function of distance to spawning habitat, hydrology, and bank stability. Distance to spawning was introduced as a polynomial covariate and hydrology (groundwater, runoff) and bank stability (moderately stable, stable) were introduced as factors with two levels each. * indicates that the variable is significant at the p<0.05 level.

(*b*) Contribution of added degrees of freedom from non-linear term compared to linear term for the medium, large and total ammocoete models. Non-linearity is tested by comparing the full model and the model incorporating distance to spawning habitat as a linear term. "df" (degrees of freedom) and deviance are the difference excluding distance to spawning habitat. * indicates significance at the p<0.05 level.

(a)			**Percent deviance explained by variables**			
Sea Lamprey Larvae	**Proportion of sites present**	**Null deviance**	**Total**	**Distance to spawning habitat**	**Hydrology**	**Bank stability**
Medium (50 –100mm)	0.24	68.21	14.61%	*9.87%	0.03%	*4.71%
Large (>100mm)	0.32	79.23	14.56%	4.35%	0.23%	*9.98%
Total larvae	0.44	86.52	19.19%	5.63%	1.70%	*11.87%
(b)	**Residual df**	**Residual deviance**	**df**	**Deviance**	**Chi square value**	
Medium Non-linearity	65	54.85	-2	-13.36	*7.99	
Large Non-linearity	65	58.98	-2	-20.25	*9.91	
Total Non-linearity	65	66.23	-2	-20.29	*7.70	

Table 10. – Coefficients for binomial generalized linear models for presence of medium, large and total ammocoetes in the Paw Paw River as a function of distance to spawning habitat, hydrology, and bank stability. Coefficients are on the logit scale. Distance to spawning habitat has two coefficients because it was a polynomial covariate with 2 degrees of freedom. Hydrology (ground-water, runoff) and bank stability (moderately stable, stable) were factors with two levels where the coefficients represented the difference with the first level included within the intercept. * indicates that the slope of the covariates are significantly different than 0, that distribution of ammocoetes in stable banks is significantly different to that in moderately stable banks, and distribution of ammocoetes in groundwater-driven hydrology is significantly different to that in runoff-driven hydrology at the $p<0.05$ level.

Sea Lamprey Larvae	Intercept	t value	Distance to spawning habitat	t value	Hydrology	t value	Bank stability	t value
Medium (50 – 100mm)	-2.479	-2.318	*-39.489	-1.239	0.313	0.443	*0.586	0.776
			-21.045	-0.867				
Large (>100mm)	-2.096	-3.241	-10.716	-1.040	0.167	0.276	*1.956	2.638
			-16.896	-1.285				
Total larvae	-1.601	-3.045	-11.926	-1.511	0.752	1.253	*1.564	2.362
			-5.153	-0.556				

Table 11. – Analysis of deviance for binomial generalized linear models for presence medium, large, and total ammocoetes in the Paw Paw River as a function of *Elliptio dilatata* and *Fusconaia flava* presence. * indicates that the variable is significant at the p<0.05 level.

			Percent deviance explained by variables		
Sea Lamprey Larvae	**Proportion of sites present**	**Null deviance**	**Total**	***Elliptio dilatata***	***Fusconaia flava***
Medium (50 –100mm)	0.24	68.21	16.05%	0.00%	16.05%
Large (>100mm)	0.32	79.23	1.40%	0.43%	0.96%
Total larvae	0.44	86.52	6.19%	0.21%	*5.98%

Table 12. – Coefficients for binomial generalized linear models for presence of medium, large and total ammocoetes in the Paw Paw River as a function of *Elliptio dilatata* and *Fusconaia flava* presence. Coefficients are on the logit scale. *Elliptio dilatata* and *Fusconaia flava* were factors with two levels (present, absent) where the coefficients represented the difference with the first level included within the intercept. * indicates that distribution of ammocoetes in sites with *Elliptio dilatata* present is significantly different to that in sites with *Elliptio dilatata* absent and distribution of ammocoetes in sites with *Fusconaia flava* present is significantly different to that in sites with *Fusconaia flava* absent at the p<0.05 level.

Sea Lamprey Larvae	**Intercept**	**t value**	***Elliptio dilatata***	**t value**	***Fusconaia flava***	**t value**
Medium (50 – 100mm)	-1.253	-3.125	0.965	1.435	-9.174	-0.512
Large (>100mm)	-0.742	-2.115	-0.043	-0.067	-0.687	-0.855
Total larvae	-0.592	-1.717	0.933	1.493	*-1.718	-2.116

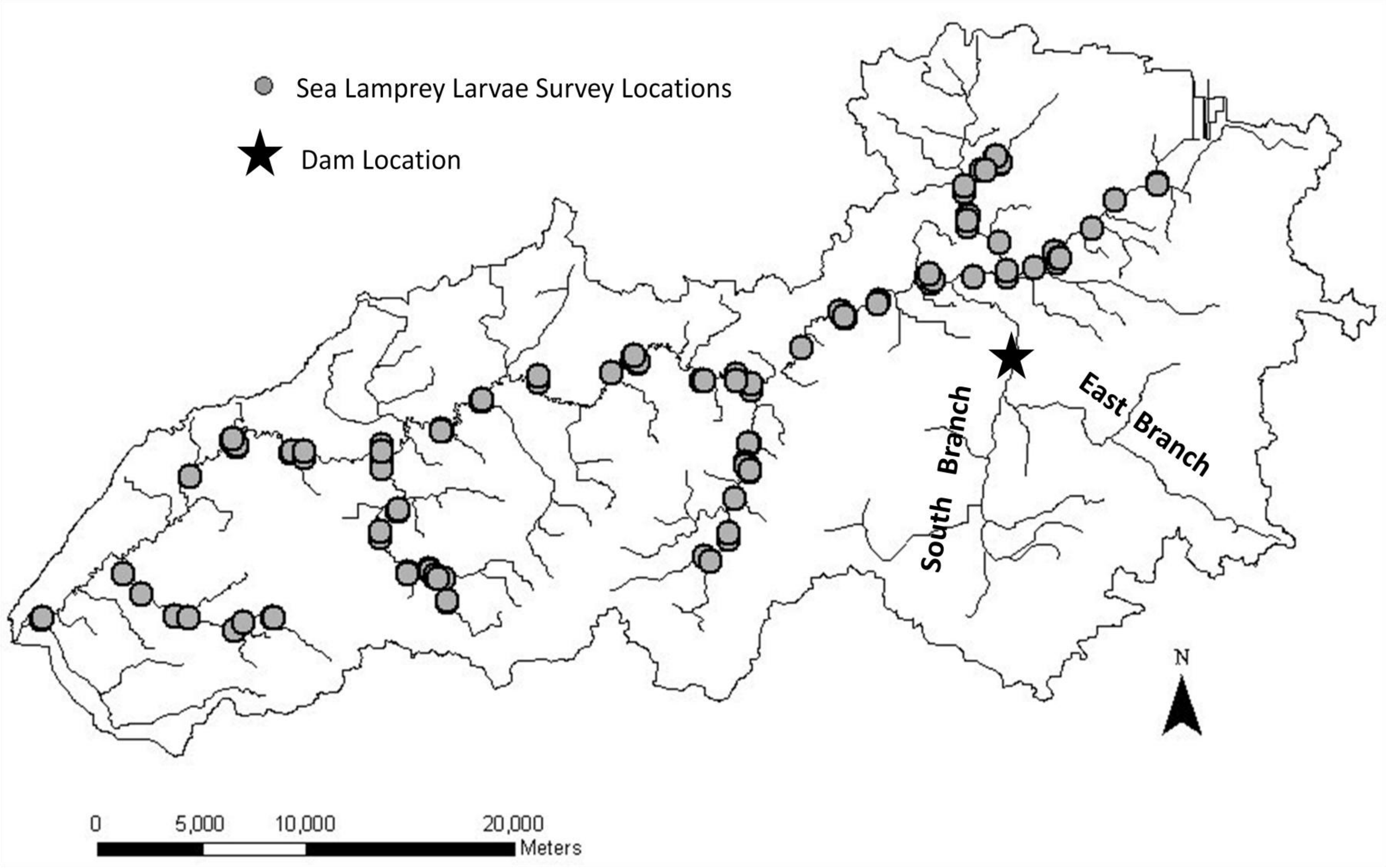


Figure 19. – Location of sites sampled during Qualitative Assessment Surveys (QAS) conducted by the US Fish and Wildlife Service's for sea lamprey larvae density and habitat. Data used for this study were collected in 1999, 2000, and 2004. No surveys were conducted in the South Branch and East Branch of the Paw Paw River as the dam is impassable to sea lamprey spawners.

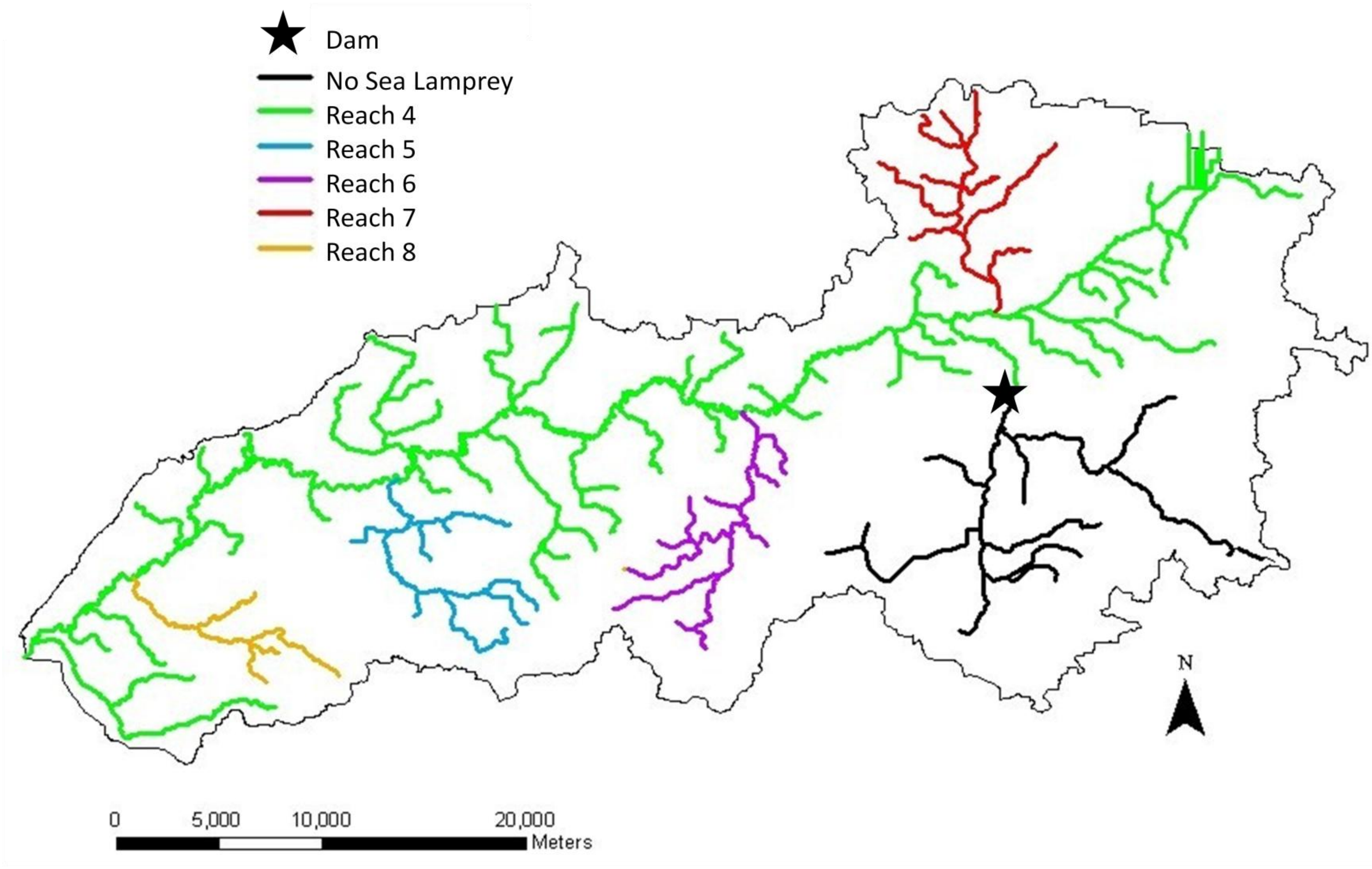


Figure 20. – Map of the Paw Paw River divided into reach units assigned by the US Fish and Wildlife Service. Sea lamprey surveys and lampricide treatments are carried out within individual reaches.

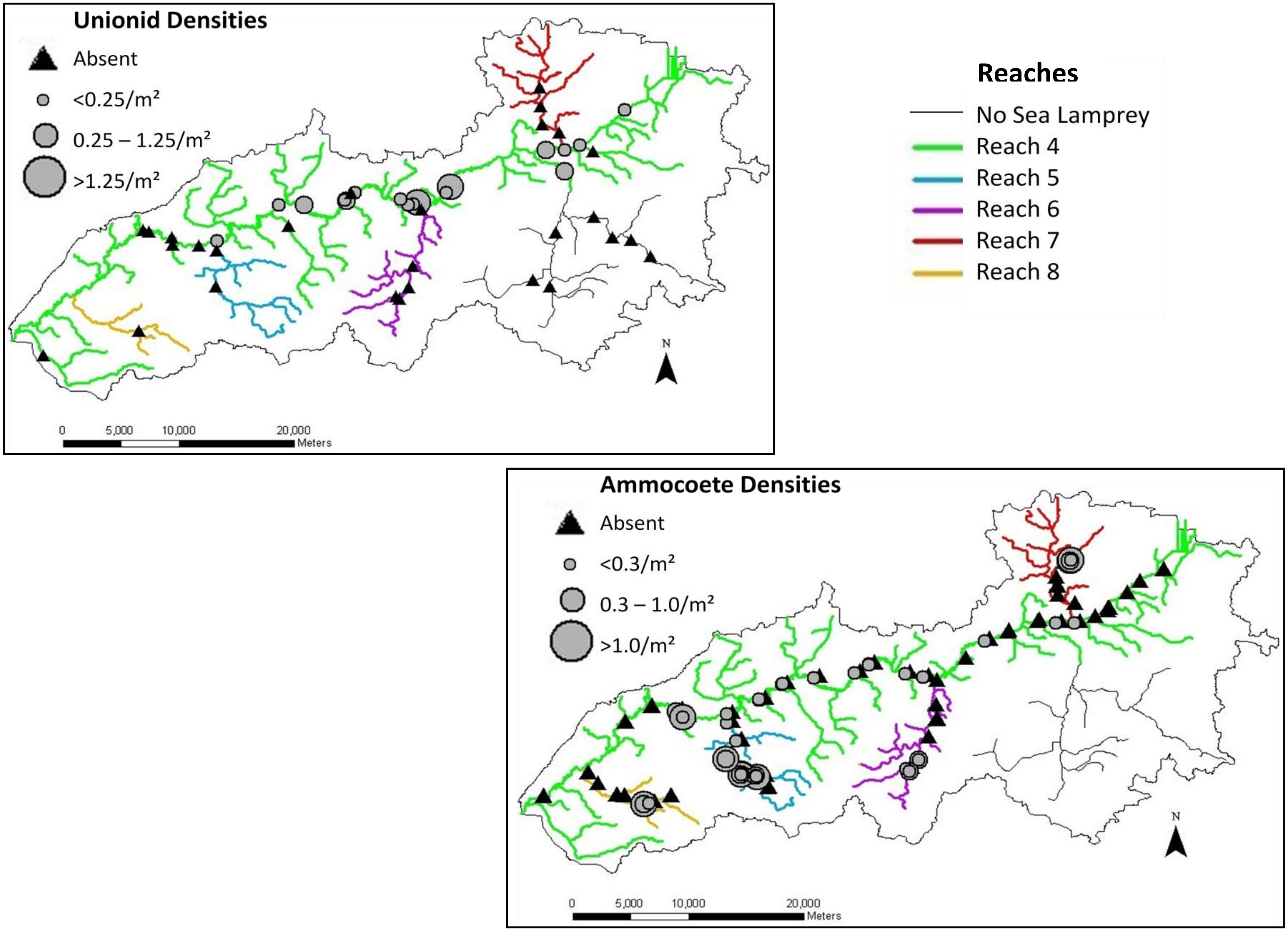
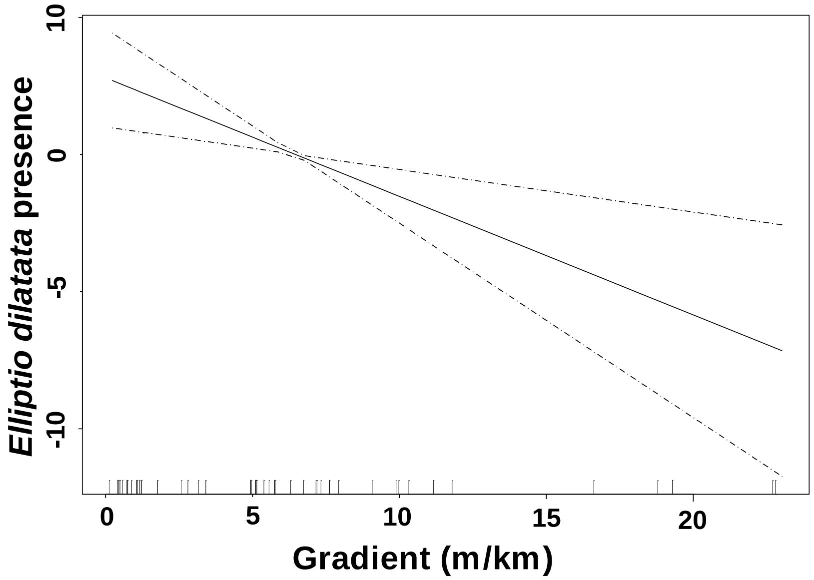


Figure 21. –Unionid densities during surveys conducted for this study within the Paw Paw River reaches defined for sea lamprey management and mean ammocoete densities recorded during QAS surveys in 1999, 2000, and 2004.



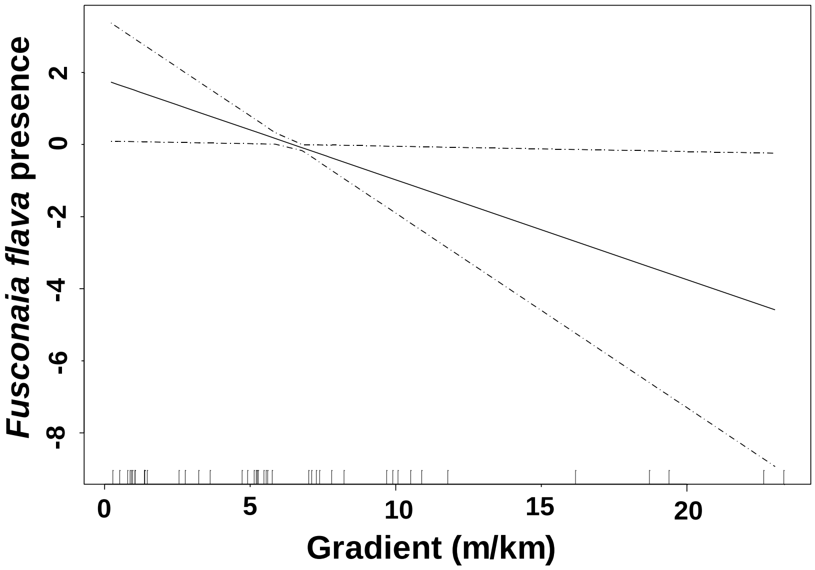


Figure 22. – Fitted probability of presence of *Elliptio dilatata* and *Fusconaia flava* in the Paw Paw River from binomial generalized linear models where presence is the function of median particle size, gradient, and bank stability. Gradient, shown here, was a significant ($p<0.05$) predictor of *Elliptio dilatata* and *Fusconaia flava* presence. The Y axis is standardized so zero represents mean probability of finding an individual. Bars on X axis represent the predictor value for each data point. Dashed line represents the 95% confidence envelopes.

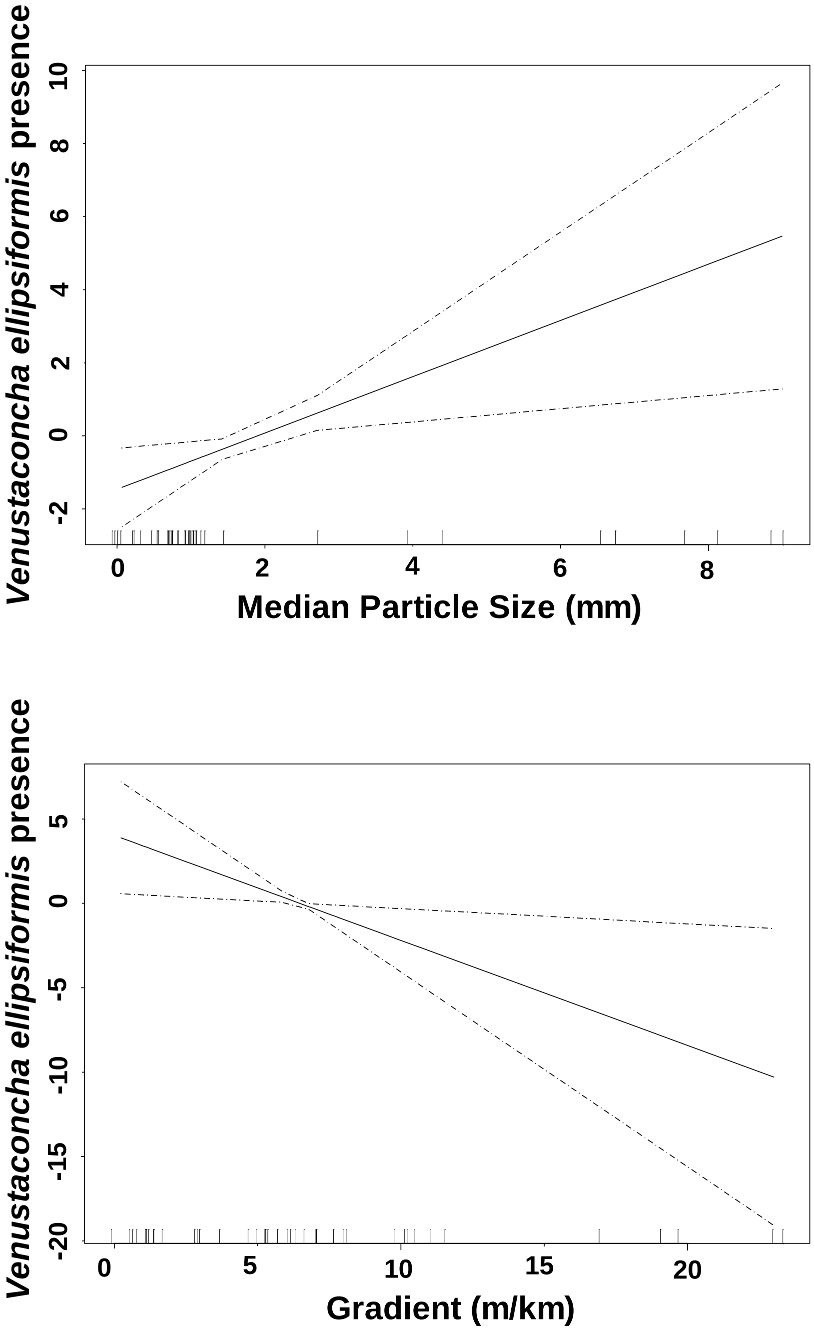
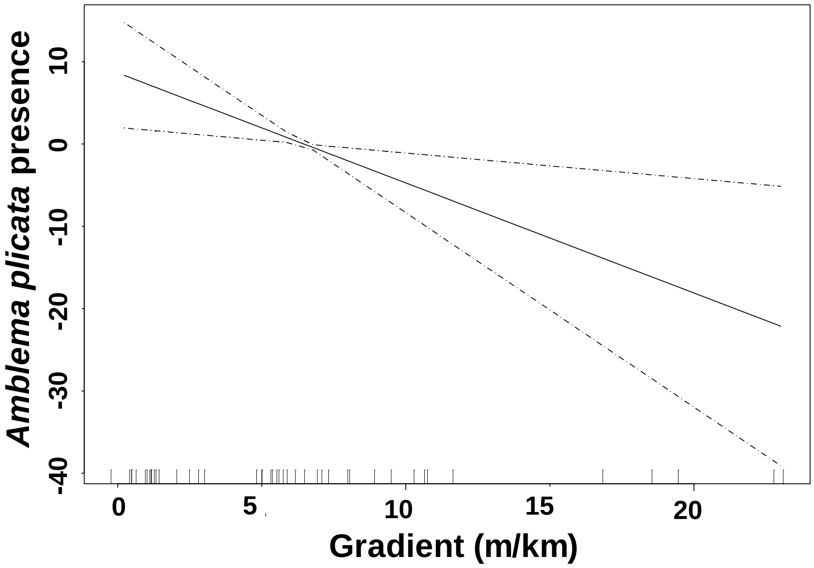


Figure 23. – Fitted probability of presence of *Venustaconcha ellipsiformis* in the Paw Paw River from a binomial generalized linear model where presence is the function of median particle size, gradient, and bank stability. Median particle size and gradient, shown here, were a significant ($p<0.05$) predictors of *Venustaconcha ellipsiformis* presence. Refer to Figure 22 for figure descriptions.



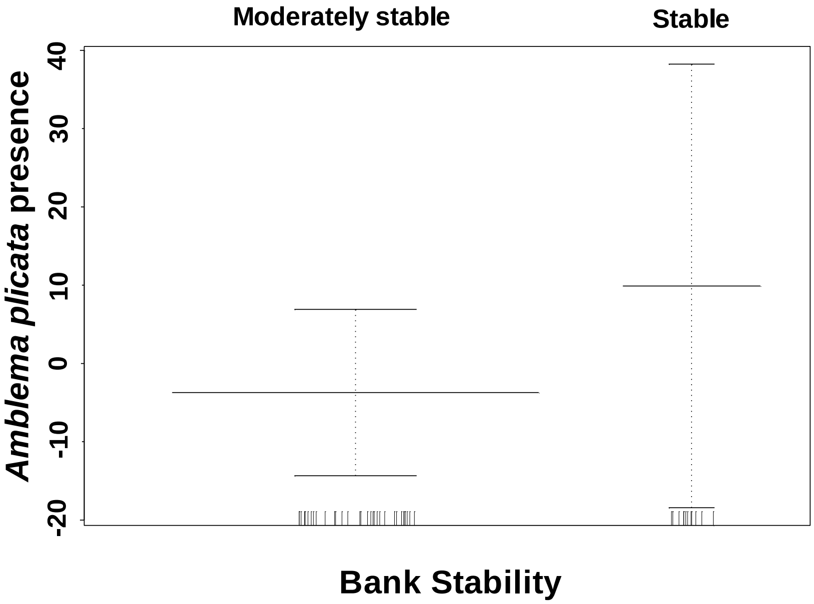
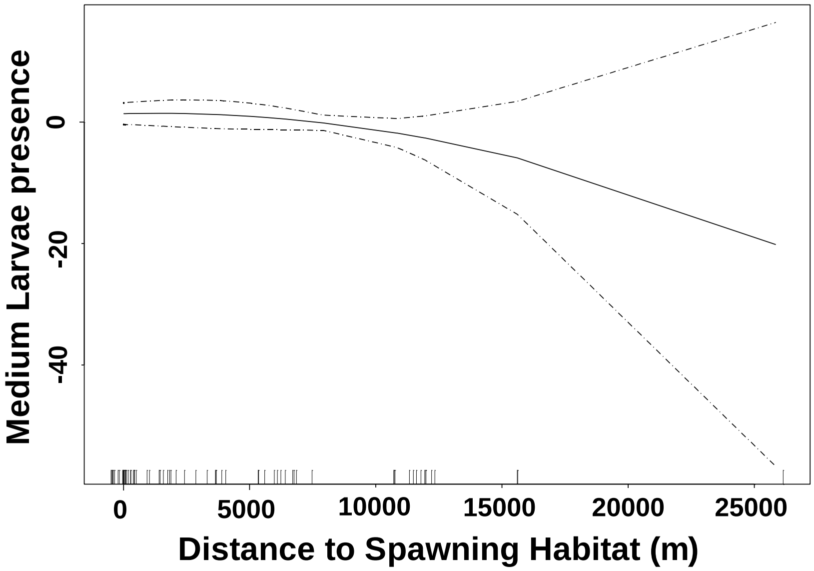


Figure 24. – Fitted probability of presence of *Amblema plicata* in the Paw Paw River from a binomial generalized linear model where presence is the function of median particle size, gradient, and bank stability. Gradient and bank stability, shown here, were a significant ($p<0.05$) predictors of *Amblema plicata* presence. The Y axis is standardized so zero represents mean probability of finding an individual. Bars on X axis represent the predictor value for each data point. Dashed lines (gradient figure) and brackets (bank stability figure) represent the 95% confidence envelopes.



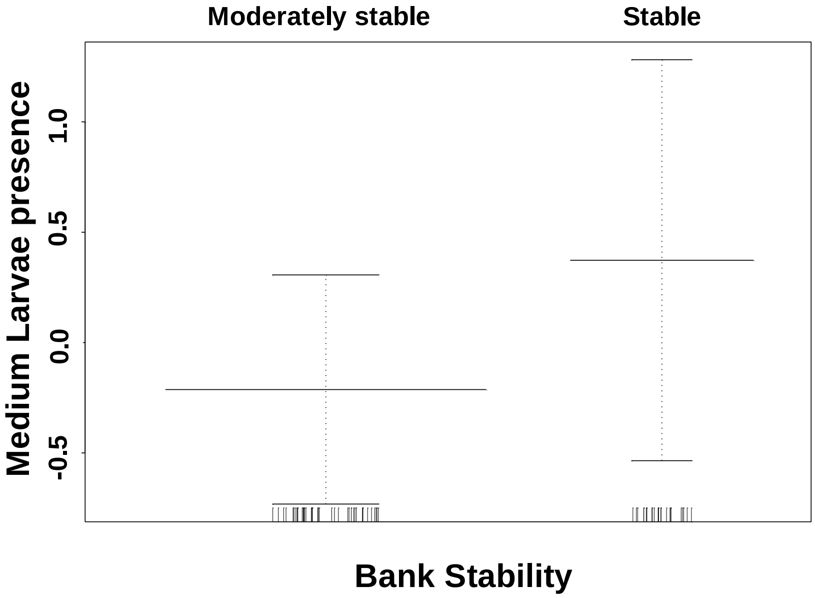
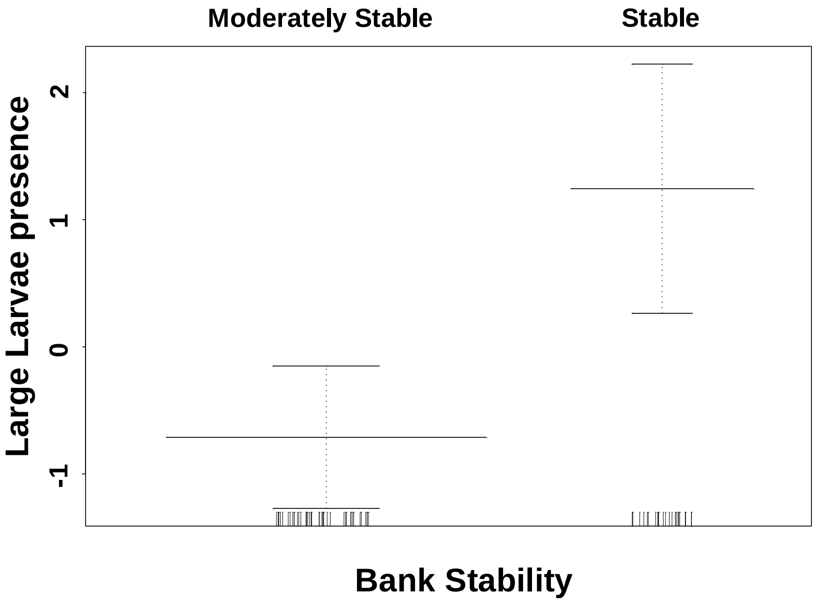


Figure 25. – Fitted probability of presence of medium sea lamprey larvae in the Paw Paw River from a binomial generalized linear model where presence is the function of distance to spawning habitat included as a polynomial of degree 2, hydrology, and bank stability. Distance to spawning habitat and bank stability, shown here, were a significant ($p<0.05$) predictors of medium larvae presence. Refer to Figure 24 for figure descriptions.



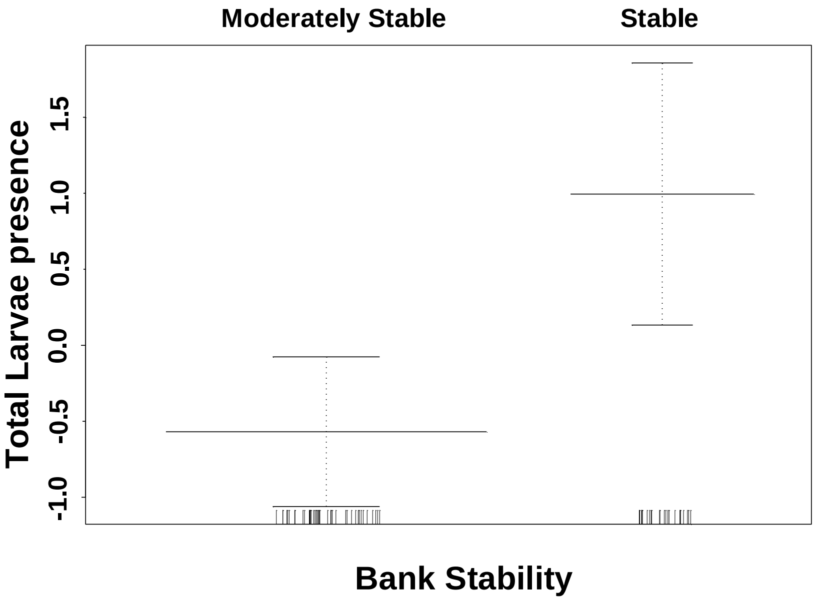


Figure 26. – Fitted probability of presence of large and total sea lamprey larvae in the Paw Paw River from binomial generalized linear models where presence is the function of distance to spawning habitat, hydrology, and bank stability. Bank stability, shown here, was a significant ($p<0.05$) predictor of large and total larvae presence. Refer to Figure 24 for figure descriptions.

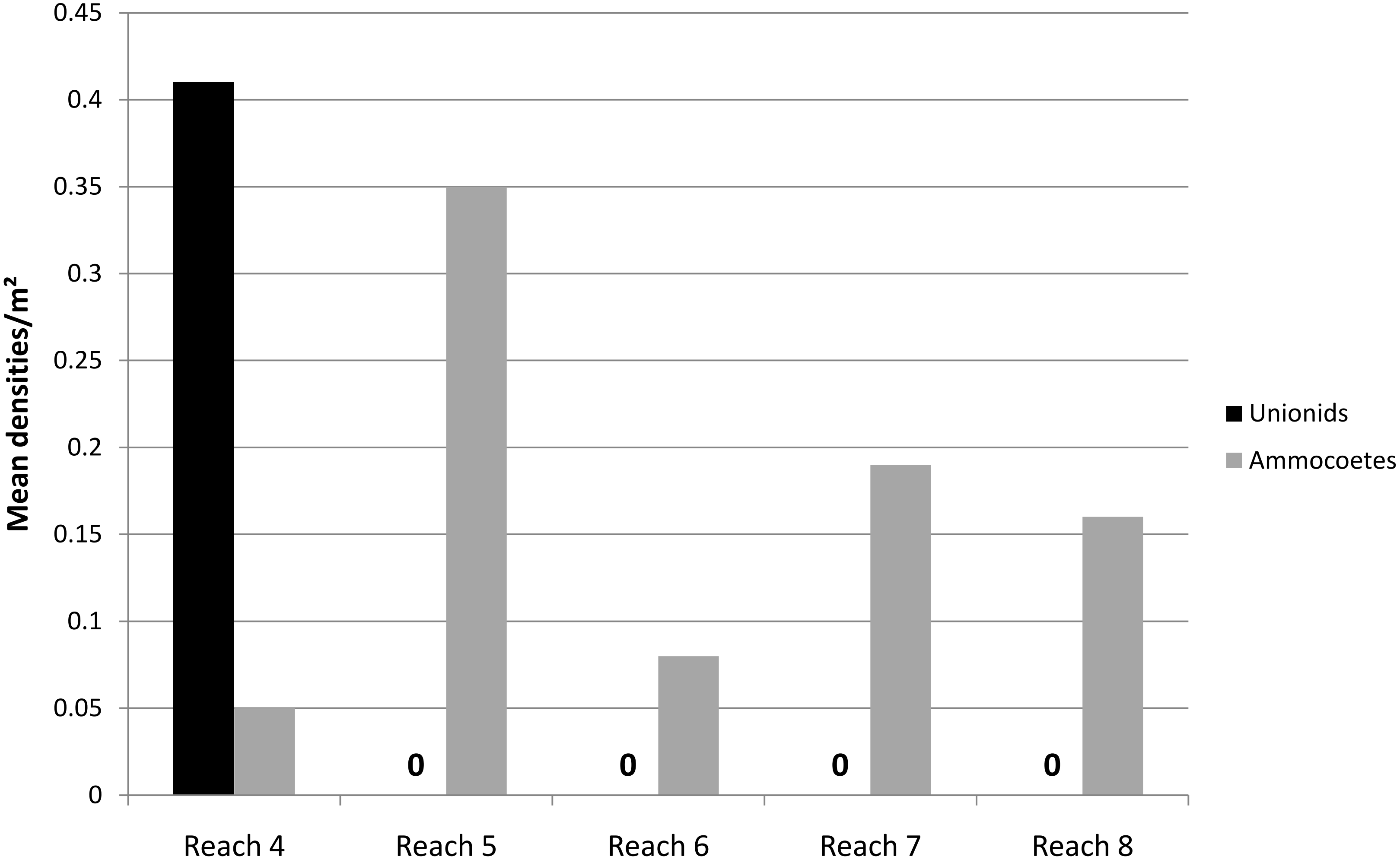


Figure 27. – Mean unionid and ammocoete densities by reach defined for sea lamprey management in the Paw Paw River. Unionid densities are from surveys conducted for this study and mean ammocoete densities were recorded during QAS surveys in 1999, 2000, and 2004.

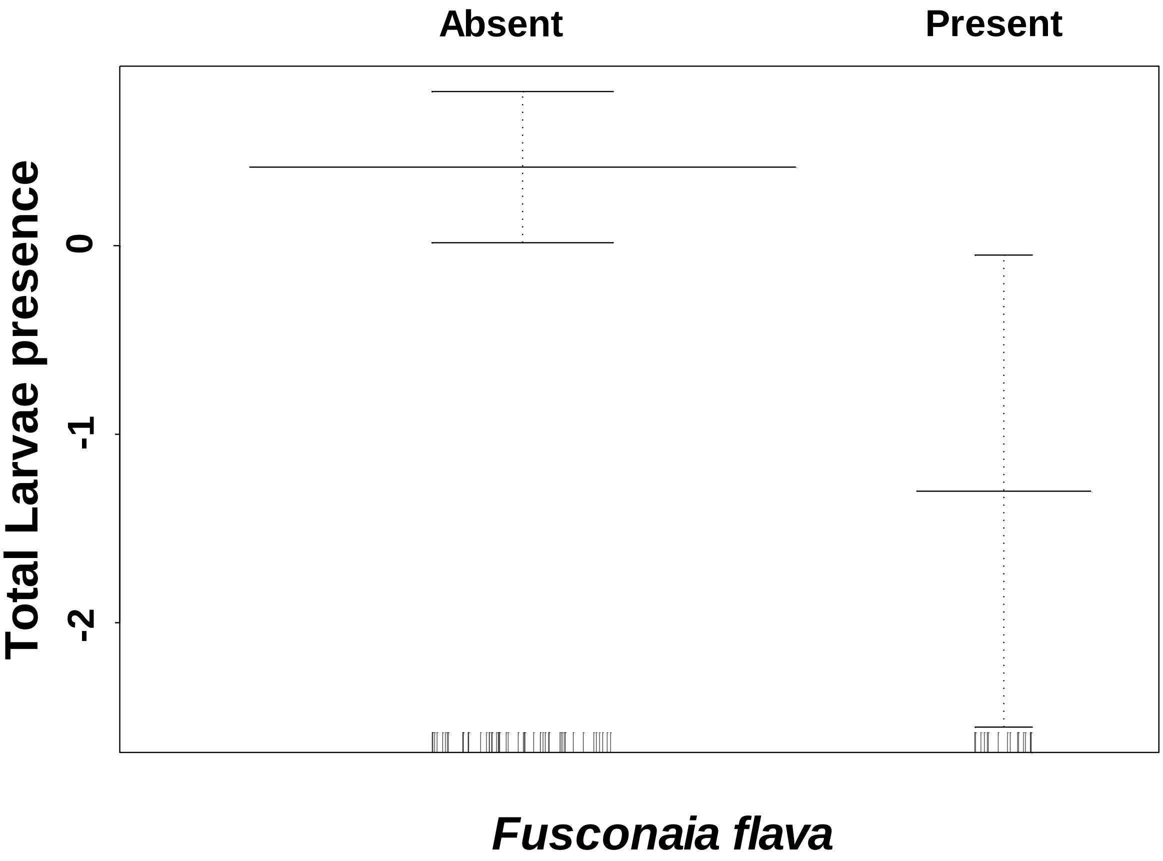


Figure 28. – Fitted probability of presence of total sea lamprey larvae in the Paw Paw River from a binomial generalized linear model where presence is the function of *Elliptio dilatata* and *Fusconaia flava* presence or absence. *Fusconaia flava* presence or absence, shown here, was a significant ($p<0.05$) predictor of total larvae presence. Refer to Figure 24 for figure descriptions.

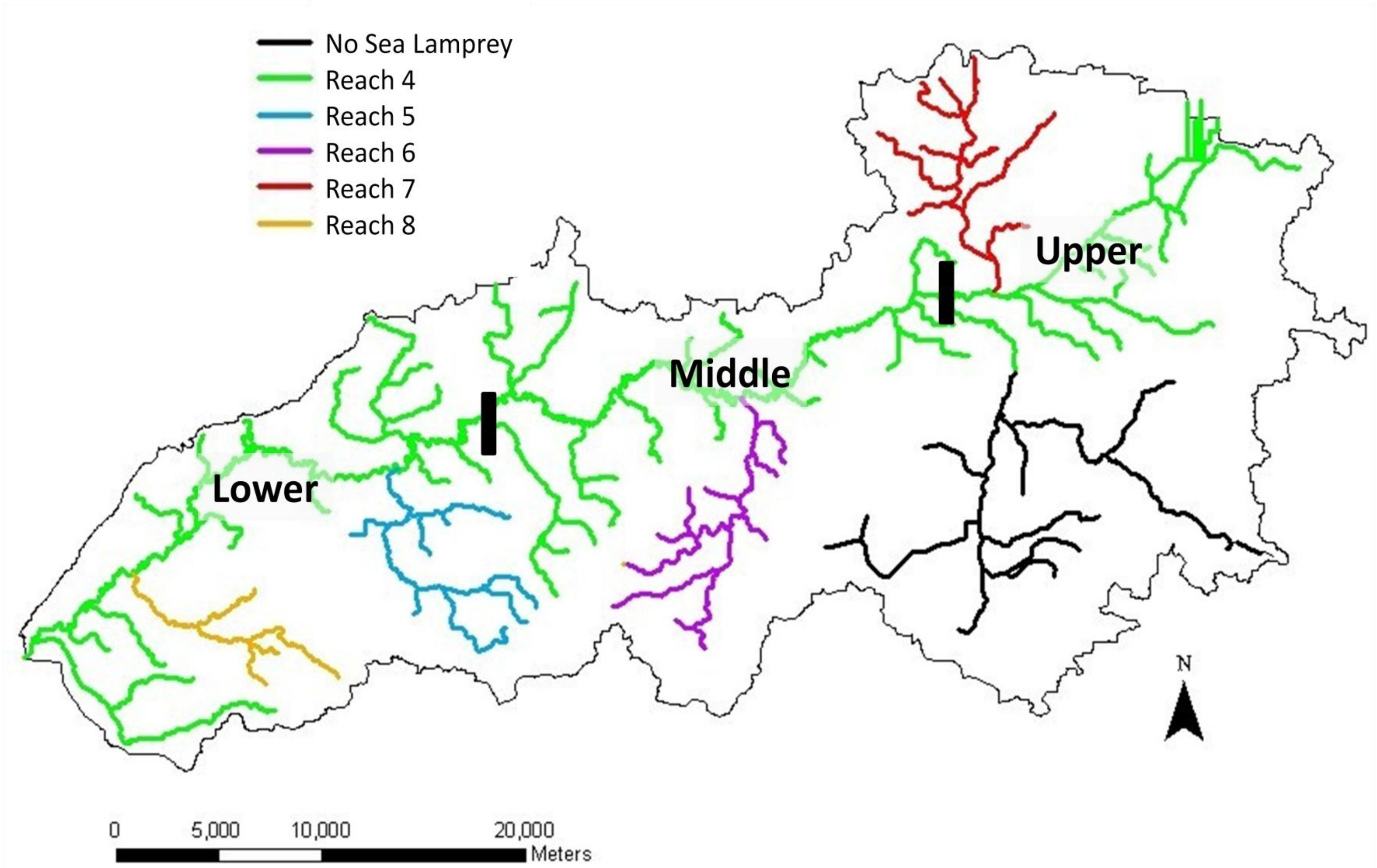


Figure 29. –Map of the Paw Paw River showing current reach units for sea lamprey management. Reach 4 shows proposed segmentation into Upper, Middle and Lower to refine sea lamprey control.

Thesis Conclusions

In summary, the results from this study indicated that unionid species in Lower Michigan streams and in the Paw Paw River tended to differ in their regional and local-scale habitat preferences. At the regional-scale, in Lower Michigan, species specific distributions with regards to hydrology, gradient, valley origin, and modeled temperature were shown in nine listed species. In the Paw Paw River, thick-shelled species with more mass (*Amblema plicata and Fusconaia flava*) tolerated smaller sand and gravel substrates and slightly unstable flows while species like *Elliptio dilatata* and *Venustaconcha ellipsiformis* were associated with larger substrates of sand, gravel and pebble mixes, and relatively stable hydrology. In the Paw Paw River, the range of habitat characteristics for selected unionids was mostly outside of the range of those for ammocoetes, hence resulting in minimal overlap of unionid mussel and ammocoete distributions. This presents potential for refining sea lamprey management towards unionid conservation.

The upper and middle portion of Reach 4 in the Paw Paw River was particularly important to selected unionid mussels and relatively unimportant to ammocoetes. Habitat was not stable enough for ammocoetes, but was within the range of habitat stability for unionid mussels. This reach was mostly runoff driven, with sand and gravel substrates, low gradients, and slightly unstable flows – not ideal habitat for larval sea lamprey, but suitable for mussels.

The Paw Paw River represents a good example for potential refinement of lampricide treatment to minimize negative effects to unionid mussels. Redefining reaches in smaller units, such as in Reach 4, so that only areas with high ammocoete densities and low unionid densities would be treated, could result in reducing treatment costs and minimizing threats to unionid conservation while still controlling the sea lamprey production to Lake Michigan. The current depressed status of the unionid community in the Paw Paw River, not as diverse as it was historically, and with the presence of shells and very few live individuals throughout the tributaries is probably representative of other systems in Lower Michigan and can be partially improved by refining sea lamprey control.

Literature Cited

Adlerstein, S., and Silverman, E. 2008. Quantitative tools to predict sea lamprey production based on habitat: Prioritizing dam removal and control decisions. Great Lakes Fishery Commision 2008 Project completion report. Ann Arbor, MI. 113p.

Anonymous. 2001. Larval assessment sampling protocol using the AbP-2 backpack electrofisher in Great Lakes streams. Great Lakes Fisheries Commission Technical Report. Ann Arbor, MI. 14p.

Applegate, V.C. 1950. Natural history of the sea lamprey (*Petromyzon marinus*) in Michigan. U.S. Fish and Wildlife Service, Special Scientific Report, Fisheries 55.

Applegate, V. C., Howell, J. H., and Moffett, J. W. 1961. Use of 3-trifluormethyl-4-nitrophenol as a selective sea lamprey larvicide. Great Lakes Fishery Commission, Technical Report No. 1. Ann Arbor, MI. 35p.

Badra, P. J. and Goforth, R. R. 2003. Freshwater mussel surveys of Great Lakes tributary rivers in Michigan. Report number MNFI 2003-15. Report to Michigan Dept. of Environmental Quality, Coastal Zone Management Unit, Lansing, MI. 40p.

Bailey, R. M., Latta, W. C., and Smith, G. R. 2004. An atlas of Michigan fishes with keys and illustrations for their identification. Miscellaneous Publications, Museum of Zoology, University of Michigan, No. 192. Ann Arbor, MI.

Bills, T. B., Rach, J. J., Marking, L. L., and Howe, G. E. 1992. Effects of the lampricide trifluoromethyl-4-nitrophenol on the pink heelsplitter. U.S. Fish and Wildlife Service, Resource Publication 183. Washginton, D.C. 7p.

Boogaard, M. A., Bills, T. D., and Johnson, D. A. 2003. Acute toxicity of TFM and a TFM/Niclosamide mixture to selected species of fish, including lake sturgeon (*Acipenser fulvenscens*) and mudpuppies (*Necturus maculosus*), in laboratory and field exposures. Journal of Great Lakes Research, 29, Supplement 1: 529 – 541.

Boogaard, M. A., Kolar, C.S. and Waller, D.L. 2004. Acute toxicity of 3-trifluoromethyl-4-nitrophenol and a TFM -1% niclosamide mixture to the giant floater (Pyganodon granis), fragile papershell (Leptodea fragilis), and pink heelsplitter (Potamilus alatus) unionid mussels and sea lamprey (Petromyzon marinus) larvae. Completion Report for Lake Champlain Fish and Wildlife Management Cooperative, Vermont Department of Fish and Wildlife, Essex Junction, Vermont.

Carman, S.M. and Goforth, R.R. 2003. An assessment of the current distribution and status of freshwater mussels (Unionidae) in the Muskegon River, Michigan. Report number MNFI 2003-18. Report to the Michigan Dept. of Environmental Quality, Coastal Zone Management Unit, Lansing, MI. 54p.

Carroll, M. and Romanek, C.S. 2006. Freshwater taphonomy: Exploring the effect of time on the trace element and stable isotope record in Unionid shells. Geological Society of America, 38, 395.

Christie, G. C. 2000. Protecting mudpuppies, protecting stream ecosystems. Forum for Stewardship and Sustained Benefits. Great Lakes Fishery Commission, Ann Arbor, MI.

Christie, G. C., and Goddard, C. I. 2003. Sea Lamprey International Symposium – Advances in the integrated management of sea lamprey in the Great Lakes. Journal of Great Lakes Research 29, Supplement 1: 1 – 14.

Christie, G. C., Steeves, T. B., Slade, J. W., Cuddy, D. W., Fodale, M. F., Young, R. J., Kuc, M., Jones M. L., and Adams, J.V. 2003. Selecting Great Lakes streams for lampricide treatment based on larval sea lamprey surveys. Journal of Great Lakes Research 29, Supplement 1: 152 – 160.

Cummings, K. S., and Mayer, C.A. 1992. Field guide to freshwater mussels of the Midwest. Illinois Natural History Survey Manual 5. Champaign, IL. 194p.

Dawson, H. A. 2007. Recruitment dynamics of Great Lakes sea lamprey (*Petromyzon marinus*) populations and implications for integrated pest management. PhD Dissertation, Michigan State University, Lansing. 118 p.

Environmental Systems Research Institute (ESRI). 2009. ArcMap v. 9.3.1. Redlands, CA.

Gilderhus, P. A. 1979. Effects of granular 2',5-dichloro-4'-nitrosalicylanilide (Bayer 73) on benthic macroinvertebrates in a lake environment. Great Lakes Fishery Commission, Technical Report No. 34. Ann Arbor, MI. 17p.

Gilderhus, P. A. and Johnson, B. G. H. 1980. Effects of sea lamprey (*Petromyzon marinus)* control in the Great Lakes on aquatic plants, invertebrates, and amphibians. Canadian Journal of Fisheries and Aquatic Sciences 37: 1895-1905.

Hart, R. A. 1995. Mussel (*Bivalvia: Unionidae*) habitat suitability criteria for the Otter Tail River, Minnesota. MS Thesis, North Dakota State University, Fargo. 60 p.

Hastie, T. J. and Tibshirani, R. J. 1990. Generalized additive models. Chapman and Hall: New York.

Hoggarth, M. A., and Yankie, J. P. 2008. Indirect effects of the lampricide TFM (3-trifluoromethyl-4-nitrophenol) on freshwater mussels in the Grand River and Conneaut Creek, Ohio. Unpublished Report, Otterbein College, Westerville, Ohio.

Holland-Bartels, L.E. 1990. Physical factors and their influences on the mussel fauna of a main channel border habitat of the upper Mississippi River. Journal of the North American Benthological Society 9: 327 - 335.

Huehner, M.K. 1987. Field and laboratory determination of substrate preferences of unionid mussels. Ohio Journal of Science 87: 29 – 32.

Johnson, D. A., Weisser, J. W., and Bills T. D. 1999. Sensitivity of lake sturgeon (*Acipenser fulvescens*) to the lampricide 3-trifluoromethyl-4-nitrophenol (TFM) in the field and laboratory exposures. Great Lakes Fishery Commission Technical Report 62. Ann Arbor, MI. 23p.

Kondolf, G. M. 1997. Application of the pebble count: Notes on purpose, methods, and variants. Journal of the American Water Resources Association 33: 79-87.

Master, L. L., Stein, B. A., Kutner, L. S. and Hammerson, G. A. 2000. Vanishing assets: Conservation status of U.S. species. Pages 93 – 118 in B. A. Stein, L. S. Kutner, and J. S. Adams (eds.). Precious heritage: The status of biodiversity in the United States. Oxford University Press, New York.

McCullagh, P. and Nelder, J.A. 1989. Generalized linear models. Chapman and Hall: London.

McLaughlin, R. L., Marsden, J. E., and Hayes, D. B. 2003. Achieving the benefits of sea lamprey control while minimizing effects on nontargets species: Conceptual synthesis and proposed policy. Journal of Great Lakes Research, 29, Supplement 1: 755 – 765.

McRae, S. E., Allan, J. D., and Burch, J. B. 2004. Reach- and catchment-scale determinants of the distribution of freshwater mussels (*Bivalvia: Unionidae*) in south-eastern Michigan, U.S.A. Freshwater Biology 49: 127-142.

Metcalfe-Smith, J. L., Staton, S. K., Mackie ,G. L., and Lane, N. M. 1997. Biodiversity of freshwater mussels in the lower Great Lakes drainage basin. National Water Research Institute. Contribution No. 97-90.

Metcalfe-Smith, J., Mackenzie, A., Carmichael, I., McGoldrick, D. 2005. Photo field guide to the freshwater mussels of Ontario. St. Thomas Field Naturalist Club Incorporated, St. Thomas, ON. 60p.

Mulcrone, R. 2006. *Venustaconcha ellipsiformis* (On-line). Animal Diversity Web, Ann Arbor, Michigan. Available http://animaldiversity.ummz.umich.edu/site/accounts/information/Venustaconcha_ellipsiformis.html http://www.natureserve.org/explorer. (Accessed: March 8, 2010).

NatureServe. 2009. NatureServe Explorer: An online encyclopedia of life (On-line). Version 7.0. NatureServe, Arlington, Virginia. Available http://www.natureserve.org/explorer. (Accessed: August 11, 2009).

Ohio Environmental Protection Agency (Ohio EPA). 2006. Methods for assessing habitat in flowing waters: Using the Qualitative Habitat Evaluation Index (QHEI). Division of Surface Water, Ecological Assessment Section, Groveport, OH. 26p.

Rankin, E.T. 1989. The Qualitative Habitat Evaluation Index (QHEI): Rationale, methods, and application. Ohio Environmental Protection Agency, Division of Water Quality Planning & Assessment, Ecological Assessment Section, Columbus, OH. 7p.

Seelbach, P.W., and Wiley, M.J. 1997. Overview of the Michigan Rivers Inventoriy (MRI) project. Michigan Department of Natural Resources, Fisheries Technical Report 97-2. Lansing, MI. 31p.

Seelbach, P.W., Wiley, M.J., Kotanchik, J.C., and Baker, M.E. 1997. A Landscape-based ecological classification system for river valley segments in Lower Michigan (MI – VSEC Version 1.0). Michigan Department of Natural Resources, Fisheries Research Report No. 2036. Lansing, MI. 51.p.

Slade, J.W., Adams, J.V., Christie, G.C., Cuddy, D.W., Fodale, M.F., Heinrich, J.W, Quinlan, H.R., Weise, J.G., Weisser, J.W., and Young, R.J. 2003. Techniques and methods for estimating abundance of larval and metamorphosed sea lampreys in Great Lakes tributaries, 1995 to 2002. Journal of Great Lakes Research 29, Supplement 1: 137-151.

Smith, D. R., Villella, R. F., Lemarie, D. P., and von Oetingen, S. 1999. How much excavation is needed to monitor freshwater mussels? Proceedings of the Freshwater Mussel Conservation Society Symposium, 1999: 203 – 218.

Smith, D. R., Villella, R. F., and Lemarie, D. P. 2001. Survey protocol for assessment of endangered freshwater mussels in the Alleghany River, Pennsylvania. Journal of the North American Benthological Society 20: 118 - 132.

Strayer, D. L. 1981. Notes on the microhabitat of unionid mussels in some Michigan streams. American Midland Naturalist 106: 411 – 415.

Strayer, D. L. 1983. The effects of surface geology and stream size on freshwater mussel (Bivalvia: Unionidae) distribution in southeastern Michigan. Freshwater Biology 13:253-264.

Strayer, D. L. 1993. Macrohabitats of freshwater mussels (Bivalvia:Unionacea) in streams of the Northern Atlantic Slope. Journal of the North American Benthological Society 12: 236 - 246.

Strayer, D. L. 1999. Use of flow refuges by unionid mussels in rivers. Journal of the North American Benthological Society 25: 271 - 287.

Strayer, D. L. 2008. Freshwater mussel ecology: a multifactor approach to distribution and abundance. University of California Press.

Strayer, D. L., and Malcom, H.M. 2007. Shell decay rates of native and alien freshwater bivalves and implications for habitat engineering. Freshwater Biology 52: 1611 – 1617.

Strayer, D. L., and Ralley, J. 1993. Microhabitat use by an assemblage of stream-dwelling unionaceans (Bivalvia), including two rare species of Alasmadonta. Journal of the North American Benthological Society 12: 247 - 258.

Strayer, D. L. and Smith, D.R. 2003. A guide to sampling freshwater mussel populations. American Fisheries Society, Monograph 8. Bethesda, MD.

ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvalue technique for multivariate direct gradient analysis. Ecology 65: 1167 – 1179.

ter Braak, C. J. F. and Smilauer, P. 1998. CANOCO reference manual and user's guide to Canoco for Windows: software and canonical community ordination (version 4). Microcomputer Power. Ithaca, NY.

TIBCO Software Inc. 2007. S-PLUS v. 8.0.4 Seattle, WA.

U.S. Fish and Wildlife Service. 1996. Nontarget mortalities observed during lampricide treatments in the state of Michigan, 1996. Michigan Department of Natural Resources, Surface Water Quality Division, Lansing, MI. 43p.

van der Schalie, H. 1938. The naiad fauna of the Huron River in southeastern Michigan. Miscellaneous Publications of the University of Michigan Museum of Zoology 40: 1 – 83.

Vannote, R.L., Marshall, G. W., Cummins, K.W., Sedell, J.R., and Cushing, C.E. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37: 130-137.

Vaughn, C. C. 1997. Regional patterns of mussel species distributions in North American rivers. Ecography 20: 107 – 115.

Vaughn, C. C., and Pyron, M. 1995. Population ecology of the endangered Ouachita rock-pockebook mussel, *Arkansia wheeleri* (Bivavia: Unionidae), in the Kiamichi River, Oklahoma. American Malacological Bulletin 11: 145 – 151.

Waller, D. L., Bills, T., Johnson, D., Dolittle, T., Luoma, J., and Hanson, M. 1997. Determination of the effects of the lampricide TFM on freshwater mussels in the Bad River, Ashland County, Wisconsin. Preliminary Report submitted to The Bad River Band of Lake Superior Tribe of Chippewa Indians, Odanah, WI. 14p.

Waller, D. L., Rach, J. J. and Luoma, J. A. 1998. Acute toxicity and accumulation of the piscicide 3-trifluoromethyl-4-nitrophenol (TFM) in freshwater mussels (*Bivalvia: Unionidae*). Ecotoxicology 7:113-121.

Watters, G. T. 1994. An annotated bibliography of the reproduction and propagation of the Unionoidae (primarily of North America). Ohio Biological Survey Miscellaneous Contribution 1. Columbus, OH. 158p.

Williams, J. D., Warren, M. L., Cummings, K. S., Harris, J. L. and Neves, R. J. 1993. Conservation status of freshwater mussels of the United States and Canada. Fisheries 18: 6-22.

Wolman, M.G. 1954. A new method of sampling coarse riverbed. Transactions of the American Geophysical Union 35: 951-956.

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